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THE MORPHOLOGY OF ARAUCARIA BRASILIENSIS

III. FERTILIZATION, THE EMBRYO, AND THE SEED

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(WITH PLATES I–III)

Since the publication of the author's account of the male (**3a**) and female (**3b**) gametophytes of *Araucaria*, certain additional facts have been observed. They will be recorded here by way of preface to the following account of the embryo and seed.

In the paper on the male gametophyte the pollen was described as lodging on the ovuliferous scale and then growing over the surface to the micropyle, and a figure was given showing a number of pollen tubes. These pollen tubes were shown pursuing a more or less direct course to the micropyle. It was stated that they sometimes crossed from the upper surface of the scale on which they had germinated to the under surface of the scale above. Since that was written EAMES has described the behavior of the pollen tubes of *Agathis* (**8**). The very interesting behavior of these tubes led me to re-examine those of *Araucaria*. It was found that while they do not, apparently, penetrate the tissues of scale and cone axis in the remarkable fashion characteristic of the sister genus, they do, nevertheless, branch much more profusely than had been supposed. It is often possible to separate a branching tube from the adjacent scales without breaking many of these branches. From this it appears that they are comparatively superficial. There is usually one main branch of the tube that goes more or less directly to the nucellus. From this numerous,

much smaller branches are given off. These branches run in all directions over the surfaces of the adjacent scales, so that when they are separated the mesh of tubes sometimes appears like a fine spider web. Numerous nuclei were distributed throughout the tubes, sometimes singly and sometimes in groups of a half-dozen or more. Aside from the body cell they all look much alike, so that it was not possible to identify the stalk and tube nuclei. The tube branches appear to grow independently of the tube nucleus or of any other nuclei. Branches were sometimes found in which no nuclei could be found at all. This was true of those of considerable length, as well as those that were just beginning to form. No cross-walls were observed in any part of the main tube or its branches. The main branch after entering the nucellus sometimes branches again (fig. 1). These branchings are very much less frequent than those outside. The available evidence indicates that only the one branch enters the nucellus.

In the majority of the tubes examined the body cell remains in the extra-nucellar part of the tube until after its division. Sperms were often observed in the tubes at the extreme tip of the nucellus (fig. 5), while very few body cells were observed within the nucellus. The mitosis of the body cell nucleus was not observed. Fig. 2 shows what appears to be the spindle lying between the two nuclei of a body cell. The nuclei are both in the resting condition and the spindle is surrounded by a delicate membrane. This membrane and its continued persistence after the daughter nuclei have reformed may be urged against this structure being really a spindle. It strongly suggests the remains of the nuclear membrane and thus suggests an intranuclear spindle. I have observed no other structures with which it could be identified, unless there may be some connection with the blepharoplast-like body referred to in a later paragraph as occurring in the cytoplasm of the male cells and the two-celled proembryo.

After the division of the body cell nucleus the two daughter nuclei do not usually separate for some time. In some cases they even enter the archegonium still closely associated. The division of the cytoplasm of the body cell follows considerably later. In some cases no distinct division has occurrred when the two male

cells have reached the archegonium. The body cell is commonly surrounded by a very faint membrane (figs. 3 and 6). In some cases this membrane is either absent or so faintly marked as to be exceedingly difficult of observation. The line of demarcation between the two male cells is in most cases not well defined. There does not appear to be a distinct membrane even when the two masses of cytoplasm are seen to be clearly separable. These male cells are not organized in definite cells as they are in cycads and *Ginkgo*.

At the time of division the two nuclei are of approximately equal size. They may both develop in similar fashion and share the cytoplasm equally (figs. 3 and 4), or one of them may degenerate even after the partial division of the cytoplasm. Fig. 6 shows a male cell or sperm clearly bounded by a limiting membrane and with the nucleus at one extremity. Across it may be seen the faint line of demarcation between the two original cells. One nucleus has degenerated and only the faintest trace of it can be distinguished in the tail opposite the functional nucleus. This degeneration is probably fairly common, for one often finds unusually large male cells in tubes in which no trace of the other one can be found. It is possible, of course, that it has retreated up the tube and into the extra-nucellar portion and so escaped observation. I incline to the opinion, however, that it has either degenerated or slipped out of the cytoplasm and become so reduced in size as to be indistinguishable from the prothallial and other nuclei.

In a previous paper (**3a**) it was stated that these male cells might possibly be motile. Since then many tubes have been dissected out in sugar solution in the attempt to prove this. The results have been entirely negative. They are apparently amoeboid (as for that matter are the male cells of some angiosperms), but there are no structural evidences of locomotor organs of any sort, nor were any rapid movements of any kind observed. Fig. 5 shows a binucleate body cell rounding a sharp corner of the pollen tube at the point where it turns back into the nucellus after having crept along over the surface of the scale. The distortion in shape is not in any way due to crowding, for there was abundant room for

it to have passed the corner without having altered its shape in the least. It was evidently creeping along the convex side of the tube and was killed just as it was rounding the corner. That the male cells actively change position and shape on their own initiative is shown also by the manner of entering the archegonium, to which attention will be called in a succeeding paragraph.

In the account of the archegonium already published (**3b**), it was stated that no ventral canal cells or nuclei had so far been observed, but that it was unlikely that they were not formed. Archegonia have since been observed in which such a ventral canal nucleus (figs. 7 and 8) had been cut off. There still remains some doubt whether this nucleus is regularly cut off. All the cases observed were in gametophytes some of whose archegonia had already been fertilized. I have not yet found a gametophyte with archegonia unfertilized where ventral canal nuclei were present. Two explanations are tenable. Either this division is delayed almost up to the time of fertilization, and the canal nucleus degenerates very quickly so as to leave no trace of itself in fertilized archegonia, or it does not occur normally, but only in those archegonia in which fertilization has been delayed beyond the usual time. Though the latter appears the less probable supposition on general grounds, the evidence available is more in accord with it. In one case (fig. 8) two small nuclei were present. The egg nucleus in this case appears small. What would ordinarily be taken for the ventral canal nucleus is larger than in fig. 7. In the majority of cases the cytoplasm of the egg in which ventral canal nuclei were found appears to be undergoing degeneration. It clumps together and has very indefinite structure. It cuts with difficulty. In some archegonia, of normal appearance in other respects, there was present a zone of fibrillar cytoplasm surrounding the very large nucleus. These archegonia were also invariably found in gametophytes with one or more that had already been fertilized. EAMES (**8**) reports the regular formation of the ventral canal nucleus in *Agathis* immediately before fertilization, and its rapid degeneration. COULTER and LAND (**6**) were unable to demonstrate its formation in *Torreya*. The expectation, therefore, is strongly in favor of its being formed normally before fertilization.

I have not been able to decide from the evidence at hand which is the more probable hypothesis.

In preparation for fertilization the egg nucleus enlarges considerably. Fibrillar cytoplasm is not uncommon in mature eggs, and sometimes, as pointed out in a preceding paragraph, forms an inclosing sheath when for any reason fertilization is delayed. The fibers of these sheaths run tangentially to the nucleus and remind one somewhat of the development of spindle fibers. They are much more abundant than is usual in the development of a multipolar spindle, and furthermore there is no reason to suppose that these mature egg nuclei are about to divide, unless for the formation of the ventral canal cell nucleus. I have seen no evidence whatever of their actually developing a spindle. Moreover, the archegonia appear to have passed their maturity already. Yet, in view of the uncertainty of the ventral canal nucleus being cut off, this possibility cannot be entirely excluded.

The nuclear membrane is well developed and incloses a relatively small mass of chromatin distributed on a fine linin network. The whole is immersed in a large volume of nuclear sap. Fig. 9 shows these facts very clearly, except that the wrinkled condition of the nuclear membrane doubtless indicates that considerable shrinkage in volume has occurred through the application of reagents. The chromatin is distributed in more or less definite strands of beadlike masses on the very delicate linin. The total number of these chromatin masses in a nucleus is very large. The total mass is also surprisingly large when one considers its volume in the fusion nucleus and in the first two nuclei of the proembryo.

Fertilization

The archegonia are mature and ready for fertilization in California about the last week of March or the first week of April. At this time the egg nucleus is usually situated a little above the middle of the archegonium. The egg cytoplasm has almost completely filled the archegonium. The vacuoles that were so conspicuous in the earlier stages of development have all disappeared. Neither starch nor other form of stored food seems to be present in the cytoplasm. As will be shown presently, the cytoplasm

itself is used up in the growth of the proembryo. The neck is composed of about 12 cells arranged in a single tier (usually). The nuclei lie at the larger peripheral end of the cells. In the pointed central end there is little cytoplasm. Often there appears to be a slight opening among the neck cells, as if in anticipation of the entrance of the sperm.

The course of the pollen tube after reaching the female gametophyte is not always direct. It frequently wanders along between the megaspore membrane and the gametophyte, eroding the latter more or less, before turning down into an archegonium. Archegonia that are apparently mature and ready for fertilization may be passed and the male cells delivered to archegonia some distance farther away from the point of entry of the pollen tube. Very commonly the archegonial chamber above each archegonium becomes overgrown, so that the tube must force its way down to the neck. Some cells are destroyed in its approach, but the way is more often prepared by the thrusting aside of the intruding cells and the consequent opening up of the previously existing passage.

When the tube reaches the archegonium its tip is thrust down into the immediate neighborhood of the neck cells. The tip is then ruptured and the male cells crowd through the narrow passage of the neck. Sometimes both male cells enter and more frequently only one can be found. The archegonia are often so crowded with cytoplasm that the entrance of the male cell causes the extrusion of some of it through the neck (fig. 10). The entry appears to be violent, for the egg nucleus is commonly driven to the bottom of the archegonium and may even be driven through the bottom. The violent displacement of the egg nucleus shows very clearly that the male cells move with considerable force, while the extrusion of the cytoplasm seems to prove that they are not forced in by the tube, as has been said to be the case in certain other gymnosperms. It seems clear from the facts just stated that these male cells are actively motile, although it is almost certain that they have no cilia or other organs of locomotion. Their large size as well as their vigor of movement makes them conspicuous among Coniferales. Such size and movement are matched only among the cycads and *Ginkgo*.

After the contact of egg nucleus and male cell the cytoplasm of the latter gradually envelops them both. Fig. 11 shows a case where both are completely enveloped in a common cytoplasm even before the nuclei have begun to fuse. In figs. 12 and 13 each nucleus is accompanied by a distinct cytoplasmic sheath even though fusion is far advanced. The egg cytoplasm is generally much disturbed by the passage of the male cell through it and does not ordinarily recover its structure. The cytoplasmic sheath around the fusion nucleus, on the contrary, continues to grow rapidly, apparently at the expense of the general cytoplasm of the egg. With the growth of the proembryo the egg cytoplasm gradually disappears, until there is commonly very little of it when the walls are formed in the former. In some cases (upper right of fig. 32) the mass of dense cytoplasm surrounding the proembryonic nuclei becomes delimited from the egg cytoplasm by a distinct membrane. So far as I have observed, this membrane has nothing whatever to do with the walls of the upper tier of the proembryo, which form later and entirely within the limits of this membrane. Fig. 31 shows a small portion of this membrane in the upper part of the figure, just above the largest cell shown. The left-hand cell shows distinctly the beginning of the formation of the walls. The wall is less clearly shown in the other cells, though the plasmatic membrane around their dense cytoplasm shows clearly where it will form. This membrane does not always form, and I am unable to see any significance that may be attached to it. The cap of cytoplasm spoken of by EAMES (**8**) as occurring above the upper tier of nuclei in *Agathis* is not ordinarily present in *Araucaria*, though fig. 27 shows a band that might be interpreted as such a structure. This figure also shows very clearly the previous delimiting membrane over the upper surface, in fact extending over that part of the embryo formed by the previously mentioned cytoplasmic cap. No distinct membrane is to be seen in figs. 25, 26, and 30, even though there is sharp distinction between the egg cytoplasm and that of the proembryo. A membrane entirely around the proembryo is shown in figs. 28 and 29. The younger stages apparently do not possess membranes of any sort.

When the male cell enters the archegonium it consists of dense cytoplasm inclosing a solid and compact nucleus. It rapidly enlarges before actual contact with the egg nucleus. At the time of contact there is much more nuclear sap and apparently rather less chromatin. The condition of the nucleus before contact is fairly well shown in fig. 16, showing (above the 2-nucleate proembryo) the second male cell. This male cell is beginning to degenerate and is in consequence somewhat more dense and homogeneous than the functional one. It should be compared with figs. 11–15. The egg nucleus contracts instead of expanding. It also appears to lose much of its chromatin. A comparison of figs. 11–15 with fig. 7, all photographed at the same magnification, will make this point clear. At the time of fusion the two nuclei are not very different in size. It is rather difficult to obtain an accurate notion of their comparative sizes because of the markedly different shapes. The egg nucleus usually remains round (figs. 11–14), while the sperm nucleus becomes concave on the side pressed against the egg nucleus. In consequence, it spreads out laterally so as to cover a third to a half of the surface of the egg nucleus. Its change of shape is accompanied by a loss of nuclear sap, but probably not of chromatin. The two nuclei remain in contact for some time, as shown by the frequency of this stage in my preparations as compared with some other stages. The manner of fusion is shown in fig. 15. A perforation between the two nuclei is formed and the gap stretches until the contents of the two nuclei are contained in a common cavity. The nuclear membrane of the fusion nucleus thus consists of parts of both the sperm and egg nuclear membranes.

The chromatin of the two nuclei enters the fusion nucleus in the form of coarse or fine nets. Fig. 15 shows the chromatin as fine granules distributed evenly throughout the two nuclei. Fig. 13 shows granules arranged in series that might easily correspond to individual chromosomes. Other preparations show various gradations between these two extremes. Whether the two masses remain separate, as is said to be true in *Pinus* (**5, 9a, 14, 15**) and some other gymnosperms, could not be determined from the available material. No preparation showing the fusion nucleus after

complete fusion and before complete division was secured. I have been forced to the conclusion that this stage must be of very brief duration.

The relative position of the two sexual nuclei varies somewhat in different archegonia. The male cell probably comes in contact with the upper side of the egg nucleus. In many cases this relative position is shifted through the violence of the impact, so that the male cell may lie more or less to one side or even far around toward the bottom (fig. 13).

The second male cell sometimes enters along with the functional one. I have seen no indications of its functioning in the manner reported for *Agathis* (**8**), or in any other manner. When it enters it soon degenerates (fig. 16). I have seen no evidence that it ever divides, as has been reported for some other conifers (**9a, 9b**).

Attention has been called to certain peculiar bodies in the cytoplasm around the fusing sexual nuclei and sometimes in that of the 2-nucleate proembryo. Fig. 15 shows two of these bodies. The one to the left may possibly be a disintegrating vegetative nucleus from the pollen tube, though I do not think so. The one lying in the cytoplasm between the nuclei certainly is not of this nature. They are not found in every cell, but occur frequently enough to be legitimate objects of curiosity. They suggest the blepharoplasts of the cycads. When they were first observed a diligent search was instituted immediately for similar structures in the body cell and the male cells before they enter the archegonium. The results were entirely negative. Fig. 17 shows one in the second male cell within the archegonium. The division of the fusion nucleus has not been observed, and it is possible that they may function here as blepharoplast-like or centrosome-like bodies.

Proembryo

The division of the fusion nucleus probably follows soon after the complete union of the egg and sperm nuclei. The resulting nuclei may lie one above the other, side by side, or in an oblique plane (figs. 17–19). They vary considerably in size, as is evident from a comparison of figs. 18 and 19. Before the next division there is a moderate increase of cytoplasm. The two nuclei

probably divide simultaneously, since no 3-celled proembryos were found. No mitoses in the proembryo have been observed, nor any trace of evidence that the nuclei divide amitotically. I have already, in former papers (**3a, 3b**), called attention to the very curious fact that almost no mitoses in the critical stages of development of *Araucaria* have been observed. It is a very curious and puzzling fact, not to say a very annoying one. SAXTON has recently called attention to a similar state of affairs in another southern hemisphere form, *Actinostrobus pyramidalis* (**18a**).

The four free nuclei may occupy almost any position with reference to one another. It has already been mentioned that the position of the fusion nucleus appears to depend on how much it is displaced through the violence of the contact between egg and sperm. It may lie near the middle of the archegonium, as it does in *Agathis* (**8**), or more generally near the bottom. The succeeding divisions take place wherever the fusion nucleus has been left. This same displacement would probably tend to conceal any polarity that the fertilized egg might possess. The commonest appearances of the proembryos are shown in figs. 20 and 21. Sometimes the four nuclei may all lie at the bottom of the proembryo, as in figs. 23 and 25. The subsequent divisions do not appear to follow any definite order nor are they simultaneous. Whether the 4 nuclei were tetrahedrally placed (figs. 20, 21), placed in a single vertical plane (fig. 23), or in a curved line around the bottom (fig. 23), or in any other position, seems not to affect the ultimate result. Irregular division continues for two weeks or more before the final arrangement of the cells in tiers. The number of cells or free nuclei at this time varies considerably. No counts of less than 32 nor more than 45 were obtained from an examination of a considerable number of embryos of about this stage. The number of proembryos showing the beginning of wall formation was so small that it cannot be certainly said that some of those with 32 free nuclei might not have had more at the time of wall formation. Many of these seemed as large and as definitely arranged as the ones with a greater number of nuclei. It seems to me, therefore, that the number of nuclei at the time of wall formation is probably variable.

After or just about the time of the cessation of free nuclear division the nuclei arrange themselves as shown in fig. 30, which is a median vertical section. It will be seen that there is a central group of nuclei arranged more or less regularly in two tiers, surrounded by a complete jacket of peripheral nuclei. These peripheral nuclei are usually more numerous on the lower side than on the upper. Even before walls are formed the lower nuclei sometimes begin to elongate, foreshadowing the formation of the cap. Fig. 32 shows a proembryo in which walls are forming about the lower nuclei, which are already set off in definite cells. The walls appear to form first in that part of the embryo which first begins elongating. In fig. 32 the lower cells formed first and began elongating while there is yet no indication of the future cells in the upper portion of the proembryo. Precisely the opposite state of affairs is shown in fig. 31, where the upper cells are elongating and forming walls while the lower cells are just forming but have not begun elongation and have only faint traces of walls around some of them.

After the complete establishment of walled cells the elongation which had already begun continues simultaneously in both the upper and lower cells. It is only after this elongation that one may properly speak of tiers, for, as already pointed out, the cells are arranged concentrically rather than in layers. Few or no divisions occur in the terminal group of cells, destined to form the cap, during this preliminary elongation, and none at all subsequently. There is a considerable increase in the upper group. They divide longitudinally, so that there are ordinarily about twice as many cells in the young suspensors as there were in the group of cells from which they were developed. The number shown in cross-section varies somewhat, but is usually not far from 20. As the suspensor cells elongate, their upper ends are thrust backward and upward (that is, in the direction of least resistance) until they encounter the firm top of the archegonium. Their upper ends ordinarily become swollen during elongation, so as to stretch the upper part of the archegonium (fig. 33). Incidentally this figure also shows that the neck is not ruptured by the entrance of the male cells and is not torn away from its mooring to the

upper part of the jacket as EAMES has shown to be the case in *Agathis* (**8**).

The cap is completely organized by the time the elongating suspensors have reached the neck of the archegonium. Owing to the greater elongation of the central cells of the cap than of those in each successive circle back of it, the cap has a much more pointed appearance than the proembryo at first exhibited. Fig. 35 shows a mature cap. It exhibits very clearly the relations of the component cells. This figure also brings out very clearly the fact that the tiered appearance of the embryo is more apparent than real, for the cap is really formed of all the cells of the peripheral layer below the suspensor. The embryonic group lies in a cup-shaped depression in the top.

The embryonic group of cells consists of a hemispherical or globular mass of small cells. There are usually 20–24 cells in the hemispheres (fig. 35), but there may be as many as 30 or even more in the globular masses. The number contained in the proembryo remains unchanged from the time they are set off and walled in until after the development and elongation of the primary suspensors.

After the organization of the walled proembryo and its preliminary development of the cap and an anchorage in the top of the archegonium, the suspensor cells begin a rapid elongation, accompanied by transverse division. This pressure of elongation maintains a firm contact of the cap with the cells in front of it. The suspensors at first thrust straight downward toward the center of the endosperm. This stage of development is probably accomplished quite rapidly, for most preparations show either free-nuclear proembryos or long, coiled suspensors (fig. 37). Usually more than one embryo starts development, about three of which start near enough at the same time to make the race for position in the center of the endosperm (fig. 36) a spirited one. When they have reached the center, the competitors coil around one another in the struggle for supremacy. One finally emerges below (fig. 37) —the victor. The others ordinarily perish without further development, though not a few cases have been seen where a second embryo had reached some such degree of development as that shown in

fig. 40 or 41. I have found no seed with a second embryo large enough to be seen with the naked eye.

Ever since STRASBURGER'S account (**23**) of the cap of the proembryo of *Araucaria brasiliensis*, it has excited comment on its apparent specialization. It has been spoken of as a protecting cap (**7, 20, 23**), but no evidence has been adduced to show that protection is at all necessary. The caps are not made of specially strong cells, nor do they show any effects of abrasion, which might reasonably be expected if they were of use as a protection. Neither do the cells of the endosperm surrounding the caps appear to have been crushed and thrust out of the way. It seems much more likely that the cells of the cap secrete a digestive enzyme. An inspection of figs. 34–37 will make this evident. Very few cells of the endosperm show any distortion from crushing, while practically all of them show the action of some corrosive agent on their contents or even in some cases on the walls themselves. I have seen no evidence, however, for thinking that the secretion of enzymes is limited exclusively to the cap. In fig. 34 it will be seen that the region of greatest cell destruction is around the embryonic region and not directly in front of the advancing tip. It is clear from fig. 37 that the cavity in which the proembryos lie continues to enlarge around the suspensors long after the cap has passed by. To put the argument in another way, the cavity should be cylindrical if solution occurs only around the cap, whereas the cavity is actually shaped like a wide-mouthed cone, showing that solution has gone on all over its surface and not merely at the apex of the cone. It is, of course, possible that this might be true and still all of the enzymes be formed in the cap, but excreted in such abundance that they fill the entire cavity with a solution of equal strength. I suspect that the matter comes to about this. The cap looks like a highly specialized structure and should in consequence have a specialized function. The proof that it does actually have a special function has not yet been adduced.

Sometime in June or July the primary suspensors have reached their limit of elongation. Then begins the third and final stage of development of the proembryo. The activities of this stage are limited to the embryonic group of cells. A rapid multiplication

of its cells is the first step. Fig. 38 shows an early stage in this growth. As soon as it begins the cap cells begin to disintegrate and are soon crushed (figs. 38 and 39). At first all the cells divide with equal rapidity. Very soon the upper cells show a tendency to enlarge, and more especially to elongate, while the lower ones continue division unabated. An early stage of this phase of development is shown in fig. 39 and a later one in fig. 40. The proembryo now consists of two regions: (1) The very actively dividing cells at the tip constitute a large apical meristem, and (2) the cells behind the meristem gradually cease division and elongate so as to produce a massive secondary suspensor which pushes the proembryo still farther down into the endosperm. After a time (a month or so) the proembryo consists of a massive suspensor and a large cylindrical body of meristematic tissue. The activity of the apical meristem practically ceases.

Embryo

Three new meristems are now developed. The first of these is picked out where the suspensor joins the main body and is to form the growing point of the hypocotyl. The other two form either side of the original growing point and quickly develop the two cotyledons. The remains of the primary meristem constitute the meristem of the stem apex, which continues dormant until some time after germination of the seed. Fig. 42 shows a longitudinal section of such an embryo some time in early September. All the regions of the embryo are now in course of development. Stem and root apices, cotyledons, and vascular tissues are clearly in evidence. These regions continue growth for two months or more before the seeds have reached the shedding stage. Growth in this period is largely confined to the cotyledons, which become very large in comparison with the hypocotyl.

The distribution of the vascular tissues in the embryo is shown in figs. 42–44. The cotyledons are traversed by 7 vascular bundles. Each of these can be traced backward to its separate union with the vascular cylinder of the hypocotyl. In the latter the procambium strands form a hollow cylinder. Just below the origin of the

bundles of the cotyledons the vascular cylinder is more or less quadrangular. The longer axis lies in the plane of the cotyledons. The other two sides are more weakly developed and bend in slightly toward the stem apex. The vascular cylinder rounds up gradually as it extends toward the root.

Resin canals are abundant in the cortex of the embryo, but do not occur in the pith or wood. There is a fairly regular circle of them three or four cells beneath the epidermis. Another definite circle occurs just outside the procambium strands. There is no definite boundary between stele and cortex, and so I am somewhat uncertain whether this ring of ducts should be attributed to the cortex or to the pericycle. Some authors (**20**) apparently speak of all the outer portion of the embryo as pericycle. I can see no good reason for this usage. The tissue is all alike at first. Then the procambium strands arise in the central region, inclosing a region of parenchymatous cells and are in their turn surrounded by a similar parenchymatous region. There is a pretty regular correspondence in number and position between the procambium strands and the resin ducts. Between the inner and outer circles there are numerous other less regularly disposed ducts. The preceding facts are shown in fig. 43, though not so clearly as I should have liked. Resin ducts occur in the cotyledons also. In the base they accompany the vascular bundles and are just below the epidermis of the outer face of the cotyledon, but not on the inner side of the bundles. Farther out toward the tips the outer ring extends completely around beneath the epidermis, in much the same way as in the hypocotyl. Resin ducts do not appear to extend upward in the embryonic mass from which the final embryo is differentiated beyond the dark line shown in the upper part of fig. 42.

In the subsequent growth of the embryo the hypocotyl changes very little, while the cotyledons elongate enormously. At the time the seeds drop from the cone axis (late November to January), the embryo is about 3 cm. long, of which the hypocotyl forms about 5–6 mm. At this time the embryo is quite straight and extends to within about 1 cm. of the tip of the endosperm. The hypocotyl is crowded closely into the apex of the seed.

After the fall of the seed the embryo continues to grow unless it becomes excessively dry. Fig. 48 shows a longitudinal section of a seed that had been stored in a tin box in my laboratory for a year and a half at least, and possibly two and a half years. The seed has continued the development of the embryo in much the same manner that would have occurred if it had been planted, except that development has gone on at a much reduced rate. Many other seeds in the same box put out roots 3–4 inches long within 6–8 months. When planted the hypocotyl emerges in the spring following the winter in which the seeds were shed. As these seeds are often shed in California before the rainy season has begun, it is evident that this intraseminal development is a means of enabling them to make the most of the growing season when it does come. It is not unlikely that in their native habitat this habit is equally useful. The seeds that did not continue growth appeared not to have done so on account of the attacks of a fungus that reduces the endosperm to a fine white dry powder. The embryos become yellow, shrunken, and waxy. The proportion of seeds failing to sprout was much the same in the box on my shelf as when they were properly planted. In fact, complete burial seems to be unfavorable to successful germination.

Endosperm and seed

During the development of the embryo important changes occur in the female gametophyte. The young gametophyte consists of comparatively large, very thin-walled cells with exceedingly scanty contents. They are multinucleate at the time of fertilization. By the time the proembryo has used up the food supplies of the archegonia and has begun to push down into the gametophyte, the cells immediately below have increased their cytoplasm markedly (figs. 34, 36, 37). The nuclei also increase in number. As the embryo advances the zone of food formation and storage precedes it. In the center of the endosperm there is left a narrow space more or less free from food storage. Toward this latter the embryos direct their course. The region of growth and storage of foods is below the archegonia. The upper region shrivels up and is crowded back into the apex of the developing seed. The

lower part of the gametophyte enlarges many fold. This growth is due in part to cell multiplication, but more largely to the increase in size of the already existing cells. As they enlarge they form and store up starch and multiply their nuclei up to 4 or 5 in almost every cell, and in some of them to twice these numbers. Fig. 46 shows nearly all of a single cell taken from about the middle of the endosperm. The light lines near the border mark the position of the delicate cell walls, which do not show in the photograph. The large oval bodies are starch grains, and the small round ones are proteids. Many of the cells are so crowded with food as to make photographs difficult. The proteid granules appear much later than the starch grains. They are not distinguishable optically much before the stage of the embryo shown in fig. 42. They never become so large or so numerous as the starch grains. Much the larger part of the growth of the gametophyte occurs during this period of food formation and storage subsequent to fertilization. At this period it is not more than 5–6 mm. in length, while at maturity it is about 4 cm. long and 15 mm. wide at the widest part. At fertilization it is broadest just below the archegonia; at maturity it is broadest at the basal end (compare fig. 48 with fig. 4 in the earlier paper [**3b**]).

After the embryo has differentiated its organs and has begun its final stage of development its cells become packed with food materials (fig. 45). The smaller round grains shown in the figure are starch. The proteids occur in very large subspherical masses. Not infrequently the large globule includes a smaller one. The inclusions are also sometimes angular and probably crystalloids. The latter are smaller than the globular ones. Peculiar dumb-bell-shaped bodies are also found included in the large proteid masses. Often one end is included, while the other projects freely from the surface. The nuclei of these cells often become very large and sometimes flattened. Two conspicuous nuclei of this sort are shown along the lower side of fig. 45.

The growth of the gametophyte does not destroy the nucellus, as usually happens among the gymnosperms. On the contrary, it continues to develop *pari passu* and forms an integral part of the mature seed coat. In fig. 48 it can easily be distinguished as a

separate layer of the seed coat, especially on the right side of the figure. Its tissues become lignified in precisely the same manner as those of the integument and scale. Fig. 47 shows a section through the developing testa at about the time it begins to become woody enough to be unsuitable for cutting in paraffin. The outer layer consists of a conspicuous epidermis filled with mucilaginous contents. Beneath this there is an irregular layer of cells with darkly staining contents, probably largely tannins. On the inner border next the nucellus there is a less conspicuous epidermis underlaid by several layers of elongated, thin-walled cells with very scanty contents. The larger part of the testa consists of the irregular cells shown in the central part of the figure. These cells become elongated and more tangled as the seed grows larger. At first their walls are very woody and tough, but not at all brittle. In the adult seed they turn brown, become much more brittle, and when dry are capable of being in part reduced to fine brown powder by crushing. The changes in the integument and nucellus are of the same kind as those occurring in the scale itself. The result is that in the mature seed all these parts have developed into a homogeneous structure, and ovule and scale have united to produce the seed. It resembles what might be expected to develop from a naked anatropous ovule.

Discussion

Araucaria and *Agathis* resemble one another very closely, differing only in minor points. They present a number of sharp contrasts to most other conifers. Pollination of the ovuliferous scale, very long and extensively branching pollen tubes, extruding nucelli, precocious division of the body cell, large actively motile male cells, and concentric proembryos will serve to recall some of these points of difference. Excepting *Saxegothaea*, with its protruding nucellus near which the pollen germinates, these features are very different indeed from the corresponding ones in the other families of Coniferales.

These resemblances to *Saxegothaea* have attracted the attention of a number of botanists (**16, 22, 24, 25a, 26**). Taken in connection with other resemblances they are sufficient to create a strong

probability of a real relationship between the araucarians and podocarps.

Though it has been generally recognized by botanists that the protruding nucellus is correlated with the method of pollination and extensive growth of the pollen tube, it does not appear to me that this very peculiar situation has received anything like the attention that it deserves. I have elsewhere (**3a, 3b**) expressed the opinion that pollination of the scale, coupled with an extruded nucellus, is more likely to indicate the retention of an ancient habit than the acquisition of a new one.

It must be admitted that we know comparatively little about the structures and affinities of paleozoic seeds and pollination devices. In the absence of present knowledge we must resort to more or less probable conjectures in our attempt to relate the already known facts. We do know enough, however, to make it very probable that the earliest known gymnospermous seeds are very far from being representative of the beginnings of the seed habit. They had already acquired numerous complexities. It is scarcely credible that the actual first seeds should have been provided with a deep and narrow micropyle, with devices to draw the pollen grains down into it and on into a chamber specially prepared for their reception by the breaking down of the cells of the nucellus. It is further to be noted that seeds of this type have in their pollen chambers pollen grains that show no signs of having possessed pollen tubes. It seems evident that this complexity of devices must have had a more or less extended history, and that to understand it we must try to conjecture the conditions and structures that would have been likely to be developed as intermediate stages between heterosporous pteridophytes and these paleozoic gymnosperms.

It is not alone that we do not know the history of the seed structures of these early gymnosperms that makes the problem difficult. The difficulties of relating the structures known in more modern plants to these ancient ones is no less difficult.

An analysis of the known facts will show that there are four distinct methods of accomplishing pollination and fertilization now known among gymnosperms: (1) the Cordaitales and Cycadofilicales

have a pollen chamber in the nucellus in which the pollen grains lodged; no pollen tubes are known and the indications are that they were not developed; (2) in Cycadales the pollen lodges in an already prepared pollen chamber in the nucellus and forms haustorial branching pollen tubes, which do not penetrate toward the female gametophyte and take no part in transferring the ciliated sperms to the archegonia; they are haustorial and nutritive in function; the way for the sperms is cleared by the gradual dissolution of the cells forming the bottom of the pollen chamber; (3) in most of the Coniferales the pollen passes down to the tip of the nucellus, where it puts out a pollen tube that is both nutritive and a sperm carrier; (4) the Araucarineae, and to a less extent *Saxegothaea*, are pollinated on the ovuliferous scale at a distance from the ovule, from which point a pollen tube grows toward the micropylar end of the ovule and there enters the protruding nucellus.

Another fact that seems to me especially significant in any attempt to account for the origin of these various habits is that in *Araucaria*, some podocarps (**13**) related to them probably, and in cycads, the embryo is not mature when the seeds are shed and keeps on growing after the seeds fall. It appears to me that this is the sort of habit one would theoretically expect to find in primitive seeds for reasons stated below. It adds strength to this supposition that Cycadales are universally recognized to be primitive plants, and that many investigators believe the araucarians to be the modern representatives, little changed in many ways, of a very ancient line and to be closely connected with the podocarps. Perhaps it will be worth while to attempt a brief analysis of the possible origins of the four classes of pollination devices mentioned above.

CYCADOFILICALES.—Whether the Cycadofilicales are more primitive than the Cordaitales is a debatable question, but that they exhibit their seeds on less modified foliar organs affords some reason for thinking that the seeds themselves are also less modified. *Physostoma elegans* (**17**) will serve as a starting-point in an attempt to work back to the origin of seeds of this type. In the seeds of this type the integument is split up into more or less divergent lobes

which do not closely invest the nucellus. The female gametophyte is covered by a very thin layer of nucellar tissue above. The pollen chamber occupies almost all of the exposed portion of the nucellus and probably laid bare the gametophyte at its maturity so that the free-swimming (probably) sperms had direct access to the archegonia.

One may suppose that when pollination first began the nucellus was freely exposed, and that the integument was either wanting or less developed than in *Physostoma*. Since these seeds were freely exposed on leaflike organs, there must have been developed, as the first necessary step to pollination, a sticky secretion on the nucellus to catch the microspores or pollen grains. It must be further supposed that the pollen grain was able to secure sufficient food from this secretion to maintain itself for such a length of time as was necessary for its further development, and until the gametophyte had broken through the nucellus and exposed the matured archegonia. It is supposable that the processes that produced the sticky secretion might in the course of time develop the habit of further destroying the cells of the tip of the nucellus to produce a rudimentary pollen chamber. The further step of eroding this chamber deep enough to allow access to the archegonia without waiting for the growing female gametophyte to rupture the nucellus would appear to be easy and logical.

During the development of the pollen chamber the integuments would be developing in the direction of greater efficiency in securing the deposition of the pollen on the tip of the nucellus. As they closed up the sticky secretion would be exuded as a pollination drop to catch the pollen. If the ovules stood upright gravity would effect the delivery of the pollen to the pollen chamber. In any case, the pollen would probably be retracted along with the pollen drop when it began to dry up. It is in this stage of development that the seeds of Cycadofilicales are found fossil. The reason (it appears to me) is that seeds that had been fertilized (or were far enough along to be fertilized soon) fell to the ground and continued their growth. If this were the case one would expect to find fossil only those seeds that had fallen too soon to be able to continue growth.

CYCADALES.—It appears that the cycads, ancient and modern, are closely related to Cycadofilicales. This relationship is not contradicted by the pollination devices, for they are so similar as to afford little difficulty in bridging over the gap. The method of deposition, as well as the presence of a pollen chamber in the nucellus, are as near alike as one could well expect. The greatest difference is the presence of a pollen tube in modern cycads. It has already been pointed out that this tube grows away from the female gametophyte and is exclusively haustorial in function. The pollen chamber itself provides access to the archegonia in just the way that we have conjectured for the preceding group. The real difficulty arises in supplying a convincing reason for the origin of a tube at all. If we are to homologize the pollen tube of cycads with the rhizoid of the germinating spore of their pteridophyte ancestors, it means that an organ that had been completely lost has been revived. Admitting the possibility, about which I am very dubious, of the revival of this ancient structure after the lapse of geologic ages, it is evident that it would be useful, subject to the laws of selection, and likely to be preserved. If pollination preceded fertilization only a short time in the earlier seeds, and the remaining processes took place on the ground, it is evident that what these ancient plants had attained was not the "seed habit," in the sense that we employ the term with reference to modern plants. They had merely attained the ovule and pollination habit. A real seed could be developed only if the seed structure were retained on the plant until its maturity (except the growth of the embryo itself). An advantage would certainly lie in early pollination of the ovule that would permit the further growth of the ovule even while the gametophytes were maturing. That this habit of pollination long before fertilization is an advantage is indicated by the fact that all modern seeds practice it, although it is difficult to imagine that the first seeds or ovules that were pollinated furnished food and protection on the exposed nucellus sufficient to maintain the male gametophyte for a year or more, as is commonly the case in modern conifers.

CORDAITALES.—The Cordaitales differ from the Cycadofilicales, among other things, in that their seeds occur in cones and not on

exposed foliar organs. It is an interesting and I think a significant question whether the pollination-habit or the cones were developed first in this group. If we assume provisionally that the cone habit did not develop until after pollination was a fixed habit, the explanation of the origin of the latter given above might be applied to this group also. The cone habit would then have been acquired while the integuments and pollination apparatus were being perfected. The difficulties of this explanation seem to me not to lie in its application to the Cordaitales themselves, but in the assumptions that must be made in deriving the Coniferales, particularly the Araucarineae, from them.

If it be supposed that the Cordaitales as a class had all reached essentially the same stage of development of the pollination devices, and that it was comparable to that already described for the Cycadofilicales, we may then seek to see just what changes must have taken place during the evolution of modern conifers. *Ginkgo* presents almost the same devices as the cycads, and we may therefore confidently assume that an explanation that will suffice for the one will prove adequate for the other.

CONIFERALES.—Excepting for the moment the araucarians and *Saxegothaea*, the modern conifers are characterized by the pollen being caught in a pollination drop and drawn down upon the tip of the nucellus or at least into the micropyle, where it germinates. The pollen tube that is produced is both haustorial and spermiferous. It grows more or less directly down through the nucellus and delivers the male cells in the neighborhood of the archegonia. It must be noted that it thus differs very sharply from the pollen tube of the cycads and *Ginkgo*, where the pollen tube is strictly haustorial and is never even entered by the body cell or its products. It is evident therefore that *either this pollen tube is one that has altered its function and completely changed its method and direction of growth or it is a different kind of pollen tube.*

As there were no pollen tubes (probably) in the Cordaitales there is no compulsion to assume that their descendants necessarily developed a tube that behaved in the manner of the cycads. *Ginkgo*, of course, would be an exception to this statement, but

may be left out of present consideration because there is little evidence that it lies in the line of direct descent to the conifers. Since the method employed in the cycads is an entirely successful one (more so than that of the conifers, in fact), there would appear to be no reason why variations from it in a direction that would be not only of no use to the plant but a positive hindrance to it would be selected and preserved, even if they should occur. It seems very unlikely, therefore, that such a change of function did occur.

If we start with the condition actually found among the Cordaitales, where pollen grains without any tubes were deposited in a pollen chamber in the nucellus, can we see any sufficient reason for the giving up of the pollen chamber and the development of the tube? One type of ovule is just as easy to pollinate as the other, for if pollen can be gotten to the nucellar tip, there would appear to be no difficulty in getting it into the pollen chamber. If it reached the pollen chamber safely and the pollen chamber broke through so as to give the swimming sperms direct access to the archegonia, it is difficult to see what would be gained by the giving up of the chamber and the formation of a pollen tube. That the conifer method is in fact inferior and would be selected against is strongly indicated by the fact that the proportional number of good seeds in their cones is decidedly less than that of cycad cones. The evidence would thus appear to be against such a derivation of the coniferous pollen tube.

If it is difficult to see any adequate reason for the evolution of the ordinary coniferous pollen tube from the conditions found in the Cordaitales, it is vastly more difficult to imagine any adequate reason for its further evolution into the araucarian tube. We must imagine not only that the pollen chamber has been given up but that the place of pollen deposition has gradually retreated out through the micropyle and back along the scale from bad to worse. JEFFREY and CHRYSLER (11) would have us believe, not only that it did actually do this, but that to compensate itself for the disadvantage it was compelled to form extensive lateral haustorial branches and to "proliferate" the two "primitive" prothallial cells. I have not yet seen any reason advanced why the nucellus, having given up the habit of forming a pollen chamber, should have

undertaken to follow up the pollen grains by protruding itself through the micropyle. A theory beset with such manifest difficulties can be accepted only if no more probable one can be found.

ARAUCARINEAE.—The araucarians have been thought by some authors to be derived from the lycopods (**20, 4a, 4b, 22a, 22b**), and by many others to be derived directly from the Cordaitales. We have seen that the pollen tube structures do not lend any support to the derivation of the araucarians from the cordaiteans *through the other families of conifers*. Whether the pollen tube structures could be derived directly is a question that we can best attack after considering the bearing of these structures on the theory of a lycopod origin.

Miadesmia (**19**) and *Lepidocarpon* (**19**), two seed-bearing lycopods, seem to me to present the most suggestive analogies of the manner in which such a seed as that of *Araucaria* may have been evolved. I do not mean to imply that these analogies are sufficient or adequate evidence for deriving the araucarians alone or conifers as a whole from the lycopods, but merely that the araucarian pollination apparatus could be easily derived from such seeds as these plants possessed, whether they belonged to lycopods, cordaiteans, or what not.

The seeds of *Lepidocarpon* were formed in cones and not exposed as in the Cycadofilicales. The same is true of *Miadesmia*. I am inclined to attribute to this fact considerable importance. Seeds that originated on a naked foliar structure would necessarily have to be pollinated on the ovule to have any chance of success at all under any ordinary conditions of plant growth. Otherwise, the ciliated sperms would have encountered almost insuperable difficulties in reaching the archegonia and would have been limited to wet weather. It seems from such considerations that Cycadofilicales and their allies have been from the first pollinated on the nucellus, but no such compulsion rests on plants which had acquired the cone habit first. The natural, easy, and probable place for the lodgment of the earliest pollen would be between the scales anywhere. There would be far less danger of the pollen blowing away before it could become effective because of its protected

situation and far greater probability of frequently finding sufficient moisture for the swimming sperms. In fact, neither of these lycopod seeds shows any signs whatever that pollen ever lodged on the nucellus. *Miadesmia* actually possesses integumentary outgrowths that appear to be designed to prevent pollen from entering the micropyle. Though these hairs would probably keep pollen from entering the micropyle, they would serve equally well to catch it and retain it near the ovule. Sperms freed here would be in a favorable position to reach the archegonia with a minimum amount of moisture, which might very well be exuded by the cone scales, just as it is today in *Araucaria*. The reasons for the *formation* of pollen tubes in this type of pollination are no greater than in the previous type, but once formed and endowed with the habit of growth toward the archegonia, they would add immensely to the probability of fertilization, and so would tend to be selected and preserved in the evolution of the seed. Such tubes would probably always have grown toward the micropyle of the ovule because of the greater opportunity of securing suitable food in that direction. They would probably branch for the same reason that fungus hyphae branch (whatever that reason may be). Probably the main branch did not at first regularly reach the nucellus, but only came to do so later, after the nucellus had acquired the habit of secreting some chemotropically active substance. Then if the pollen tubes in search of food ever came to penetrate the nucellus before it had been broken through by the female gametophyte, they would furnish a more direct and easy route for the swimming sperms to the archegonia than for them to be freed outside the ovule as in the earlier stage. An advantageous habit of this sort would be likely to be preserved. We thus attain the state of affairs illustrated by the araucarians.

It is perhaps worth while pointing out that, in the above argument, *the various changes are not supposed to have occurred because they would be advantageous, but having occurred fortuitously to have been preserved because they were advantageous*. In contrast, the theory outlined above (11) of the derivation of pollen tubes among the conifers and araucarians requires *the derivation of disadvantageous changes and their selection and preservation notwithstanding*.

Moreover, it requires the further derivation of other structures (proliferation of the prothallial cells) to compensate for the disadvantages.

It is comparatively easy to derive the pollination apparatus of the ordinary conifers from the araucarian type by reduction, for it can be shown that each step would be an advantage, and so likely to be retained whenever it chanced to occur. In the first place, any change that would bring the pollen grains nearer the micropylar end of the ovule would shorten the distance to be traveled and so be an advantage. *Agathis* shows such a change, and there are abundant reasons for thinking it less primitive in other respects than *Araucaria*. *Saxegothaea* shows a still further stage of reduction, and there are also good reasons of other sorts for believing that it too is related to the araucarians and derived from them. The podocarps and pines illustrate the final stage where the pollen tube forming grains reach the inclosed nucellar tip before germinating. Once the pollen was deposited directly on the nucellus, changes tending to cover the nucellus by the integument and to draw the pollen down the micropyle by means of a pollination drop would be further advantages in the way of further protection to the germination tubes from drying, as well as some advantage in closing up the micropylar orifice in the maturity of the seed.

As we have seen that it would be easy to derive the Pinaceae from the araucarians so far as the seed and pollination habits are concerned, and next to impossible to reverse the order, we may now inquire whether it is possible to derive the araucarians from the Cordaitales directly in respect to the same structures. There are abundant evidences that among paleozoic gymnosperms of both great groups the nucellus either protruded from the nucellus or projected far into it. So far as I have been able to find from the literature available to me they all show pollen chambers. I suspect that this preponderance of evidence in the published accounts is due in part at least to the general opinion that pollen chambers are primitive, and so this feature has been exploited. It is conceivable, at any rate, that some of the paleozoic gymnosperms did not have pollen chambers and were not pollinated on the nucellus, but on the

scale. If such evidence should be forthcoming, the line of argument that has been used in connection with the lycopod seeds could be equally applied to the Cordaitales. The cordaitean seeds were formed in cones, and I should strongly expect that some of them were pollinated on the scale instead of the nucellus.

The theory would run something like this. When the seed habit was developed, the plants were in the midst of acquiring the cone habit. Pollination would therefore differ in nearly related plants. The ones that first perfected the pollination habit would be likely from the first to be pollinated on the nucellus. The ones forming cones first probably acquired thereby the habit of pollinating the scale. Some of these may have deposited the pollen so near the nucellus that they soon passed through the intervening stages and so show no special differences from those that always had had the pollen on the nucellus. The history of the pollen chamber would be the same as that already outlined for the Cycadofilicales. Whether these ancient plants that gave rise to modern conifers were more like araucarians or other modern conifers in other respects cannot, of course, be decided on these grounds. It does seem to me that the mesozoic conifers very probably did resemble the araucarians in respect to the seed and pollination habit. This might be equally true whether they resembled the araucarians in their vegetative structures or were more like the Abietineae, as has been vigorously maintained in recent years by some anatomists (**10**).

The theory of the pollen tube above outlined is applicable to the structure of the male gametophyte itself. There is nothing to be explained away, as must be done if we attempt to derive the araucarian type from the pine type (**11**). The numerous prothallial cells are not then to be thought of as something to be explained away, but as what is left of the ancient prothallus. A figure (**2**, fig. 2) from Miss BENSON'S paper on *Lagenostoma* seems to me to be capable of another interpretation than the one given by the author. The figure shows a number of pollen grains in the pollen chamber. At the upper right of the figure is a group of one large and several small cells. The large cell is labeled "a sperm," and the smaller ones are said to be probably fungal

cells. I should like to suggest that they strongly resemble a group of prothallial cells about a body cell or sperm as they appear in *Araucaria*. So far as it goes, it seems to me, the evidence is that there were prothallial cells in the paleozoic pollen grains, notwithstanding that eminent botanists have interpreted the evidence to the contrary (7).

I have elsewhere (3a) called attention to the very large male cells of *Araucaria*, and EAMES has recently (8) shown that they are present in *Agathis* also. A further peculiarity in their formation is exhibited by *Araucaria brasiliensis*, in that the division of the body cells occurs a long time before fertilization and not about simultaneously (7) with the division of the central cell a few days before fertilization. This division usually occurs outside of the nucellus a month or even two months before the pollen tube has actually reached the archegonia. Not only are the male cells long-lived, but they appear to be more active and independent than those of most conifers. This appears to me to be a primitive and unspecialized behavior, and one that would be unlikely to be derived secondarily from the condition now obtaining in the pines.

The male cells of *Araucaria* pass through the neck of the archegonium without injuring it. COULTER and CHAMBERLAIN (7) assert that the pollen tube of the Pinaceae destroys the neck, though LAWSON (12c) has recorded that the pollen tube of *Sciadopitys* passes between the neck cells. Among the Taxaceae the neck cells are sometimes destroyed (*Torreya*, COULTER and LAND 6), and sometimes the male cells pass through without injuring them (*Phyllocladus*, Miss YOUNG 26), just as in *Araucaria*. In *Agathis* (8) the male cells enter the top of the archegonium to one side of the neck cells, which are thereby broken loose from their anchorage to the jacket. In *Podocarpus* the necks appear to be broken through by the neck, though SINNOTT'S (21) statement is not specific as to whether the neck cells are destroyed or not. In *Cephalotaxus* (12b) the neck cells are probably destroyed by the entrance of the tube between them. In *Cryptomeria*, which externally resembles some species of *Araucaria* very closely and has other suggestions of affinity as well, the male cells are said (12a) to pass between the neck cells, but to injure them in doing

so. *Araucaria* finds again its closest resemblances among the Taxaceae. The habit of entering the archegonium between the neck cells without injuring them is an old one, dating back to Archegoniatae generally. The habit in the araucarians of liberating the male cells outside of the archegonium and allowing them to enter it under their own power of movement is doubtless more primitive than that prevailing among the Pinaceae, where the tube actually delivers the male cells inside the archegonium in many cases.

The female gametophyte is very similar to that of most conifers. Attention has been called to the apparently peculiar method of wall formation in the transformation of the free-nuclear state to the walled prothallus. Since that was written (**3b**), SAXTON has published an account of the life history of *Tetraclinis articulata* (**18b**), in which he shows a photograph (fig. 6 of his paper) in which three of the nuclei occupy a position in what is elsewhere supposed to be the wall of the forming alveoli. Possibly this may indicate that walls are formed in this plant in the same way as in *Araucaria*.

The multinucleate condition of the prothallus at fertilization time is not peculiar to *Araucaria*, being now recorded in several other genera (*Agathis*, *Cryptomeria*, etc.). It is probably more widespread than the literature indicates at present.

The late stage at which the ventral canal nucleus is cut off, and the lack of any trace of a wall are certainly not evidences of primitive behavior. In fact, there are very few evidences that the female gametophyte has lagged in its development behind conifers in general. That is, it seems to me, as it should be. The male gametophyte has retained a lot of primitive characters, because they are associated with the habit of pollinating the scale. These influences do not affect the female gametophyte, and it has therefore gone on in the course of evolution much as other conifers have done.

The persistence of the male cytoplasm in the egg has now been recorded for a number of genera of the Araucarineae, Podocarpineae, Taxodineae, and Cupressineae, but I have seen no record of it among the Abietineae. The majority of these records relate to genera (*Agathis*, *Phyllocladus*, *Podocarpus*, *Torreya*, and *Cephalo-*

taxus) that have suggestive resemblances in other respects to one another.

EAMES (**8**) has laid special stress on the fact that in *Agathis* the fusion nucleus remains in the center of the archegonium and that its divisions are limited to a restricted part of the egg cytoplasm. He looks on this as a specialization. I should be inclined to minimize the importance of this feature, for in *Araucaria* division occurs wherever the impact of the male cells has left the egg nucleus. Neither is the restriction a noticeable feature further than is determined by the fact that the proembryonic free nuclei are restricted to the limits of the male cytoplasm that envelops them.

The irregular division in the proembryo, the indefinite number of nuclei formed, and the method of their arrangement distinguish *Araucaria* rather sharply from the Abietineae, though some or all of these features are paralleled among the other tribes.

The number of cells in the proembryo before elongation, and the time of wall formation vary widely. Abietineae usually, at least, have four tiers of four cells each. In the Cupressineae the cells are usually fewer and not so regularly arranged. Among the Taxaceae the numbers run much higher (18–32) and the arrangement is still less regular. Walls form somewhere about the 8-celled stage in Pinaceae, but at widely different stages among the Taxaceae.

In all other recorded conifers, excepting *Actinostrobus* (**18a**), the proembryo is arranged in more or less regular vertical tiers and the growth is downward. In the araucarians the embryo is not tiered, but concentric at the time walls are formed. It takes on a pseudo-tiered appearance later through the elongation of the upper cells of the concentric outer layer to form the suspensor and the lower ones to form a cap. In this respect the proembyro is unique, though *Cephalotaxus* (**12b, 23**), *Sciadopitys* (**17**), and some species of *Podocarpus* (**21**) resemble it in having a cap below the embryo cells. In neither of these, however, is the embryo group completely surrounded as in the araucarians. These resemblances do not contradict a relationship between araucarians and taxads, nor do they add very much strength to the evidence for it. The structure of the proembryo is so different from that of the Abietineae that it is not easy to see how it could have been developed from it.

Notwithstanding the opinions (**8, 23**) expressed by other authors as to the specialization of the proembryo of the araucarians, I am inclined to think that too much stress has been placed on the appearance it presents after elongation has begun. At that time the very definite cap, the suspensors, and the inclosed embryo group give it an appearance of specialization that is not representative of its method of development. As I have pointed out in a preceding paragraph, this very definite structure arises from a group of free nuclei that do nothing in a definite and regular fashion. The number of nuclei is indefinite, the arrangement is that of an irregular mass, the order of wall formation varies, in short nothing is definite or fixed except that the upper and lower nuclei of the mass will elongate and result in the production of a proembryo in which the position and function of the various cells appear to have been planned with the greatest care. The course of development is, in fact, far less regular and definite than that of the Abietineae, though the result is far more striking.

The formation of a secondary suspensor region from the base of the mass of cells developed from the embryo group is a feature that has not been recorded for other conifers, so far as I have been able to discover from the literature available. The nearest approach to it is in *Torreya taxifolia* (**6**), another taxad, where there is said to be a wave of elongation beginning with the second tier and involving the successive tiers downward until finally cells formed from the embryo groups are involved. It is not unlikely that this feature may be found less rare than the records at present indicate, for our knowledge of the later development of the embryo is still very meager in conifers generally.

Conclusions

1. The structure and development of the pollen tube, processes of fertilization, and the structure and development of the embryo are such that it seems extremely improbable that they could have been derived from the analogous structures as represented in modern Abietineae.

2. The structure of the seed and pollination apparatus of the araucarians could be readily derived from the type of seeds or ovules represented by such lycopods as *Miadesmia*.

3. There is some reason to suppose that some of the Cordaitales may have had ovules of the same general type as the lycopods just mentioned. If so, they were probably pollinated on the scale and might have given rise to modern conifers.

4. It would be possible to derive modern conifers from a mesozoic stock which had ovules and pollination apparatus comparable to that now possessed by the araucarians.

Summary

1. Pollination occurs on the scale at a distance from the nucellus.

2. The pollen tube is very long and gives rise to many small lateral haustorial branches. It combines features of conifers and cycads to a certain extent.

3. Reasons are adduced to show that this is probably an extremely primitive form of tube, having come down from very remote times little changed.

4. The body cell divides in the extra-nucellar part of the tube a month or more before fertilization. The central cells of the archegonium divides very late or perhaps not at all, except in cases of delayed fertilization.

5. The male cells are very large and unusually active, as well as long-lived.

6. Blepharoplast-like bodies are found in the male cytoplasm.

7. The male cells pass through the neck without injuring the cells.

8. The male cell comes into violent contact with the egg and frequently displaces it.

9. The free nuclear divisions of the proembryo are restricted to the male cytoplasm that surrounds the fusion nucleus, which persists and grows with the proembryo.

10. The male cytoplasm around the older proembryo may be surrounded by a membrane.

11. The number of free nuclei in the embryo varies from 32 to 45 or perhaps more.

12. When walls form the free nuclei are arranged concentrically.

13. The upper peripheral nuclei form the suspensor, the lower ones the cap, and the middle girdle elongates to unite cap and suspensor.

14. The central cells of the proembryo alone take part in forming the embryo.

15. In the growth of the embryonic group the cap is thrust aside and a cylinder of meristematic tissue is organized.

16. The upper portion of the embryonic cylinder functions as a secondary suspensor.

17. The definitive embryo is organized out of a portion of the cells arising from the development of the embryo group of the proembryo.

18. It is dicotyledonous, has resin ducts in the cortex but not in the wood, and is stored full of food materials (large proteid granules and smaller starch grains).

19. The cells of the prothallus become very large and crowded with food.

20. The nucellus persists and becomes a part of the testa of the seed.

21. The embryo continues intraseminal growth after the seeds are shed.

22. It is concluded that, so far as the pollination apparatus and seed structure are concerned, the Araucarineae could be derived from the lycopods, or perhaps from the Cordaitales, but not from the Abietineae. The latter might be derived from a primitive mesozoic stock resembling the araucarians in respect to these features.

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EXPLANATION OF PLATES I–III

FIG. 1.—A pollen tube branching after entering the nucellus; the tip of the tube is just at the upper border of the figure.

FIG. 2.—A part of the body cell, showing part of the upper male nucleus and what appears to be the remains of the nuclear spindle concerned in the division of the body cell nucleus; the male nuclei are in the resting state, but the cytoplasm has not yet begun to divide.

FIG. 3.—The two male nuclei in a body cell whose cytoplasm has not yet completely separated into distinct male cells; ×250.

FIG. 4.—Two male nuclei in a pollen tube running horizontally between the nucellar cap and the female gametophyte; the cytoplasm is unusually scanty and shows no sign of division, nor does either nucleus appear larger or more active than the other; ×250.

FIG. 5.—A binucleate body cell rounding a sharp corner of the pollen tube where it turns back from the surface of the scale to enter the nucellus; a part of the pollen tube wall is shown above and another part in the bend on the right; ×250.

FIG. 6.—A fully formed male cell or sperm about half-way down the pollen tube; the nucleus is at the forward end and a fragment of the degenerating nucleus that should have formed a separate male cell out of the part of the cytoplasm above and to the left of the cleavage furrow; ×250.

FIG. 7.—The egg nucleus and disintegrating ventral canal nucleus; ×250.

FIG. 8.—Upper end of an archegonium with a large ventral canal nucleus (at the top), a small egg nucleus (bottom), and a small extra nucleus between; ×250.

FIG. 9.—A mature egg nucleus showing the dense chromatin masses distributed on the delicate linin network and to a less extent in contact with the nuclear membrane; the wrinkles in the nuclear membrane are doubtless due to the effects of the reagents used in preparation; ×560.

FIG. 10.—The neck of an archegonium through which a pair of male cells has entered; note that the neck has not been ruptured, though the passage is

very much smaller than the diameter of a male cell; the figure also shows how the egg cytoplasm has been crowded out through the neck by the entrance of the male cells; ×250.

FIG. 11.—Fertilization: the male nucleus is above; both nuclei are enveloped already in the male cytoplasm, which is distinguished from the egg cytoplasm around it by being much denser; this figure shows the only case observed in which the male nucleus is larger than the female; ×250.

FIGS. 12 and 13.—Two consecutive sections through a male and female nucleus in the act of fusing; the male nucleus is to the left of the figure; the nuclear membrane has broken down in the middle region of contact (fig. 13), but not throughout (fig. 12); each nucleus is enveloped in a distinct sheath of cytoplasm, probably derived from the kinoplasmic layer sometimes surrounding the egg nucleus, as well as from the male cytoplasm; ×250.

FIG. 14.—A median section through two nuclei in which the nuclear membrane had not yet broken down, showing how the male nucleus flattens out and applies itself to the curved surface of the egg nucleus; ×250.

FIG. 15.—Fusion of two nuclei showing the fine-grained nuclear contents and the weakening of the nuclear membranes; two blepharoplast-like bodies are also shown; the left-hand one may be, possibly, a vegetative nucleus in an advanced stage of degeneration; ×250.

FIG. 16.—The second male cell in an archegonium: the male cell is cut in the median plane, but only one of the two nuclei of the proembryo below is shown; the dark portion in the center is the nucleus crowded full of large masses of chromatin-like material; around it is seen the zone of male cytoplasm appearing lighter than the surrounding egg cytoplasm or the inclosed nucleus; this cell has probably become considerably changed through degeneration; ×250.

FIG. 17.—Another section through the same archegonium as the preceding, showing one of the blepharoplast-like bodies in the edge of the male cytoplasm and a nearly median section of the 2-celled proembryo; ×250.

FIG. 18.—Median section of a 2-celled proembryo; ×250.

FIG. 19.—Another 2-celled proembryo; ×250; figs. 17–19 show that the first division may occur in any plane, horizontal, vertical, or oblique.

FIG. 20.—Median section of a 4-nucleate proembryo; ×250.

FIG. 21.—A 6-nucleate proembryo; ×250.

FIG. 22.—A 5-nucleate proembryo; ×250.

FIG. 23.—A 4-nucleate proembryo with all the nuclei in nearly the same vertical plane and at the bottom of the cytoplasm; ×250.

FIG. 24.—A 9-nucleate proembryo; ×250.

FIGS. 25–29.—Proembryos with 15–40 nuclei variously arranged, but none with exactly 16 or 32; ×250.

FIG. 30.—A 45-nucleate proembryo, with the nuclei properly arranged for wall formation; the cap nuclei are already beginning to elongate; ×250.

FIG. 31.—The formation of walls and elongation of suspensors before the cap cells have begun to elongate or have completed wall formation; ×250.

FIG. 32.—Wall formation and elongation in the cap cells before either elongation or wall formation has begun in the suspensors; a small part of the membrane that sometimes forms above or even around the proembryo is shown at the upper right of the figure; ×250.

FIGS. 33 and 34.—A proembryo cut full length, showing all its parts after the elongation of the suspensors has begun; fig. 33 shows the expanded top of the suspensors crowded up against the neck of the archegonium; the archegonium jacket membrane is much stretched but has not broken nor has the neck been ruptured; fig. 34 shows the suspensors and the progress of destruction of the cells of the gametophyte; ×62.

FIG. 35.—Tip of a proembryo, showing the bottom of the suspensors, the group of embryo-forming cells, and the cap; note that the embryo is not properly a tiered one, and that the cell contents of the three regions are exceedingly similar; the walls of the cap cells are also seen not to be specially thicker or otherwise prepared for mechanical penetration; ×250.

FIG. 36.—Three proembryos in competition for the favored position in the endosperm; the multinucleate condition of some of the endosperm cells is also shown; the fine grains in these cells are starch and the large light colored patches are vacuoles; ×62.

FIG. 37.—The struggle for supremacy during which the proembryos coil around one another and greatly erode the gametophyte; ×20.

FIG. 38.—The beginnings of growth in the embryonic group of cells; the suspensor cells lose their cytoplasm and become distended, and the cap cells shrink and degenerate; ×175.

FIG. 39.—Further growth in the embryo group: the cap has been crushed and is being thrust to one side; cell division is more rapid in the tip region of the future embryo, while the upper cells are beginning to elongate, foreshadowing the production in that region of the secondary suspensor; a few cells of the primary suspensor are shown at the top; ×250.

FIG. 40.—The secondary suspensors pushing the meristematic apex deep into the endosperm; note the massive character of the secondary suspensor when compared with the slender primary one; ×62.

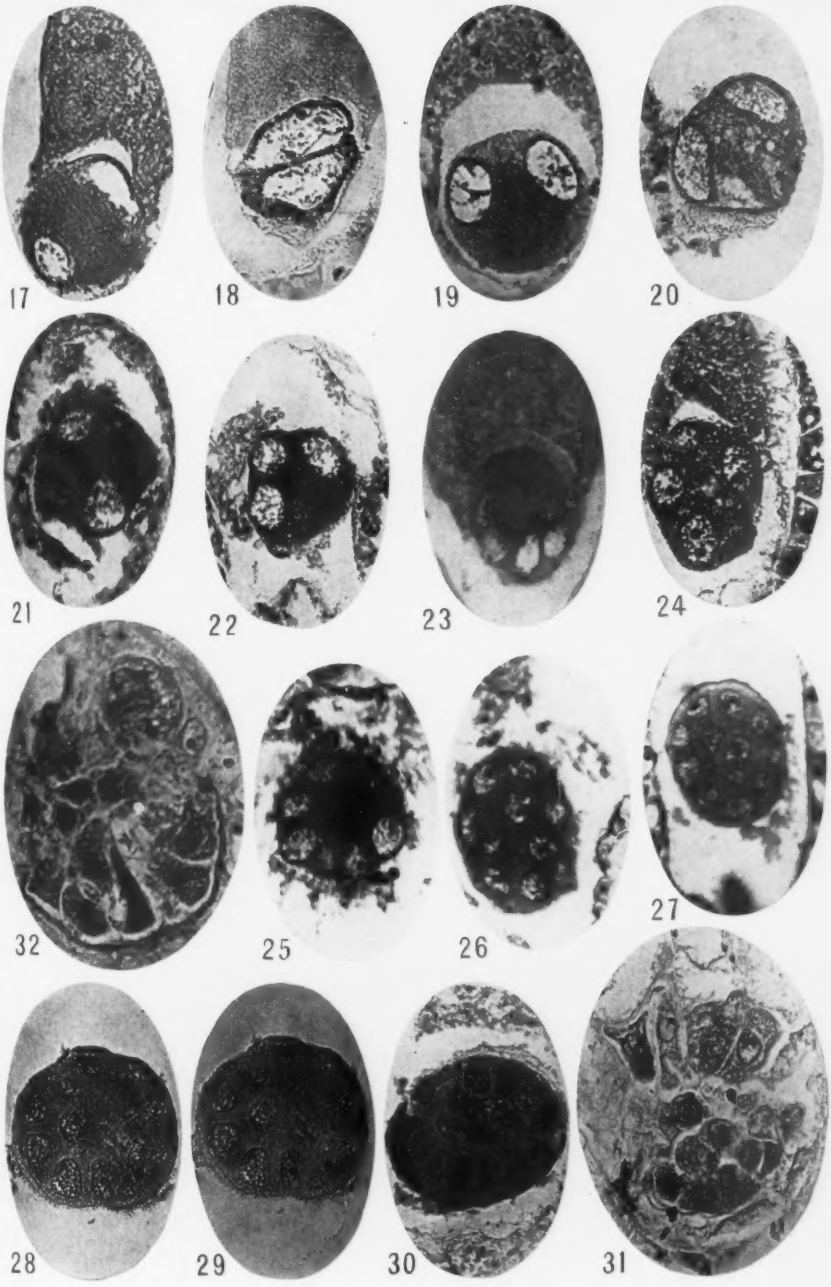
FIG. 41.—A later stage when the meristematic region has become large; the differentiation of the body regions shown in the next figure will follow shortly after the stage shown in this figure; ×20.

FIG. 42.—An embryo just after all the main body regions have been differentiated; ×7.

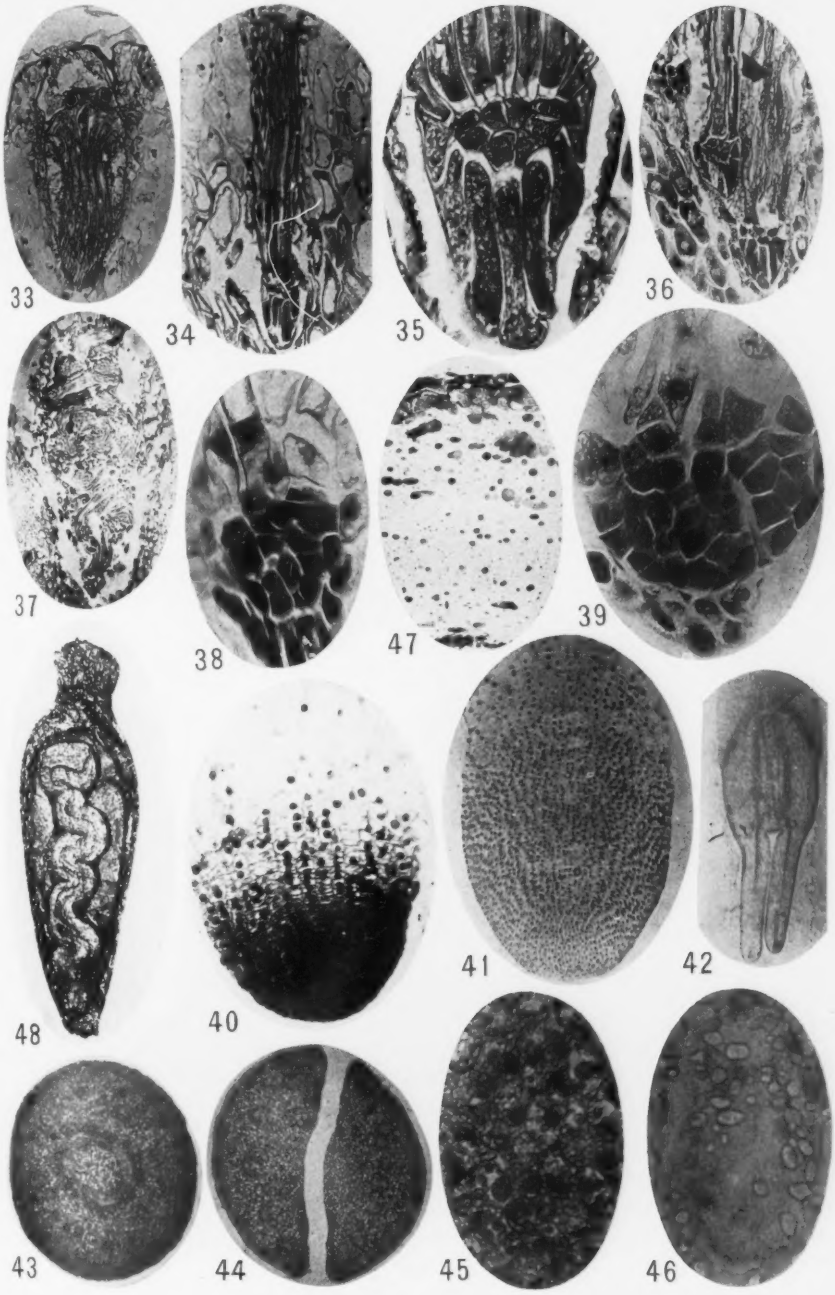
FIG. 43.—Transverse section through the hypocotyl of a nearly mature embryo, showing the vascular ring, resin ducts, and cells crowded full of starch and proteids; ×15.

FIG. 44.—Section through the cotyledons; ×15.

BURLINGAME on ARAUCARIA



BURLINGAME on ARAUCARIA



BURLINGAME on ARAUCARIA

FIG. 45.—Cortical cells from the embryo filled with small round starch grains and large proteid globules; ×250.

FIG. 46.—A single cell from the middle region of the endosperm adjacent to the embryo, showing the large oval starch grains and the tiny round proteid globules; the light lines mark the position of the delicate walls which do not show in the photograph owing to their not having been stained; ×250.

FIG. 47.—Section through the integument, showing the three layers; the central irregular cells later become woody to form the firm brown testa of the mature seed.

FIG. 48.—Longitudinal section of a seed that had been kept for over a year in a tin box in laboratory; it shows how growth of the embryo continues after the fall of the seed, even under comparatively unfavorable conditions; natural size.

THE ARCHEGONIUM OF SPHAGNUM SUBSECUNDUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 199

GEORGE S. BRYAN

(WITH PLATES IV–VII)

This paper is planned as the first of a series on the life history of *Sphagnum subsecundum*, the work being undertaken through interest in the Sphagnales aroused during a course in the special morphology of Bryophytes under Dr. W. J. G. LAND at the University of Chicago. It is hoped that this investigation may not only bring to light new facts in the life history of *Sphagnum*, but when completed may enable us to determine more accurately the position of the Sphagnales in the phylogeny of the Bryophytes.

Field study

The first stage in this undertaking, that is, securing material for study, has been something of a problem in itself. The impression prevails, in some quarters at least, that *Sphagnum* seldom bears sex organs. For example, CAMPBELL (**1**, pp. 163–164) in a general discussion of the Musci says: "When the plants are dioecious it sometimes happens that the two sexes do not grow near together, in which case, although archegonia may be plentiful they fail to be fecundated and then no capsules are developed. This no doubt accounts for the extreme rarity of the sporogonium in many mosses, although in other cases, e.g., *Sphagnum*, it would appear that the formation of sex organs is a rare occurrence."

On the other hand, those investigators who have made studies of the sex organs of *Sphagnum* seen to have had little difficulty in securing material. LEITGEB (**8**) alone reports his study of the archegonium hampered by lack of material.

Again, there is disagreement as to whether or not the archegonial branches have characters by which they may be distinguished. As is well known, antheridial branches on approaching maturity are marked by their coloration. Have the archegonial branches such a well defined character? CAMPBELL (**1**, p. 177), referring

to the Sphagnales, says: "The archegonia are found at the apex of some of the short branches at the summit of the plant, which externally are indistinguishable from the sterile branches." CAVERS (**2**, p. 295), on the contrary, says: "The female branch grows for some time in the same way as an ordinary sterile branch, but the leaves visible from the outside of the branch become rapidly longer in passing from below upward, so that the branch takes the form of a loose, tapering, pointed bud, deep green in color, and stands out sharply from the vegetative branches associated with it."

Furthermore, there is some disagreement as to the time of the appearance of sex organs. According to SCHIMPER (**10**), antheridia are produced at any time, but are most abundant in autumn and winter. WALDNER (**11**) found mature antheridia and archegonia under the snow in February. GAYET (**3**) reports having spent much time searching for archegonia in the winter, but only in the spring did he find them developing. However, he emphasizes the point that he does not wish to say archegonia are not produced at all in the winter, but rather that it is only in the early spring time one finds them being formed in the greatest abundance.

To summarize, we find: (1) sex organs are believed by some to be of rare occurrence; (2) there is disagreement as to the recognition of archegonial branches; (3) there is some uncertainty concerning the time of the production of sex organs.

To investigate these points in regard to *S. subsecundum* we have made a careful study of a bog covering about 20 acres near Mineral Springs, Indiana, 40 miles south of Chicago. This place was selected for several reasons. It contains enough water in the spring to escape being burned over, the annual fate of many bogs in the vicinity of Chicago, hence the study could be carried on without fear of having the material injured by fire. Also in previous years some sporophytes had been noted here. Furthermore, polsters of a *Sphagnum* (later identified by Mr. E. J. HILL as *S. subsecundum*) were well scattered through the bog, affording a wealth of material.

Active work was begun the first week in November 1912. It soon became evident that *S. subsecundum* here studied is dioecious, and that when the sex organs are approaching maturity both

male and female plants have well marked characters. The antheridial heads are decidedly globose and show variations in color from yellow brown to red brown, occasionally almost black. The archegonial heads are less globose, have a somewhat flattened aspect on top, and show no unusual coloring except the conspicuous bud at the growing point in the center of the head. This bud varies in color from yellow brown to red brown. An analysis of the bud reveals archegonia almost mature on short side branches near the apex of the main axis, the coloring matter being in the perichaetial leaves surrounding the organs.

A careful study of the whole bog and others for several miles about disclosed the fact that not a single sterile head of *S. subsecundum* could be found. Sex organs were everywhere in vast numbers. In order to determine whether or not such a condition might be unusual, and to provide abundant material for study, developments through winter, spring, summer, and autumn of 1913 were closely followed; and again in the autumn of 1913 the sex organs appeared in the same vast numbers.

As far as *S. subsecundum* in the vicinity of Mineral Springs is concerned, we conclude therefore (1) that sex organs are not of rare occurrence; (2) that both antheridial and archegonial heads on approaching maturity are distinctly characterized by coloration; (3) that antheridia and archegonia begin to develop in August and September respectively, the antheridia always appearing first.

A brief statement of time relations in the developmental process of the archegonium as observed in the autumn of 1913 may be of interest. Young stages were first noted on September 16 and continued to appear for approximately four weeks. By October 25 the youngest archegonia were beginning the formation of canal cells, while the oldest were almost mature. At this time the coloring of the perichaetial leaves began to be noticeable. By November 15 the canal row had broken down in some of the oldest archegonia. Those archegonia which have not reached maturity on the advent of cold weather develop slowly through the winter. In the spring, therefore, at the time of the disappearance of the snow, it is possible to find stages having 7 or 8 canal cells, with the ventral cell not yet divided.

Methods

For this investigation almost daily killings were made, from the middle of September to the middle of November. The killing agent used was 0.25 chrom-acetic, cold, and heated to various temperatures up to 52° C., the best results obtained being at about 30° C. At this temperature there was practically no plasmolysis in the delicate young stages, and the quick penetration made certain the securing of any figures that might be present in the material. The higher temperatures were not satisfactory, causing more or less plasmolysis and leaving the material difficult to stain. Safranin in combination with Licht Grün, and Haidenhain's iron alum hematoxylin were used as stains.

Development of the archegonium

HISTORICAL

The archegonium of *Sphagnum* has been the subject of a number of investigations. Of the early papers the most important is the elaborate monograph of SCHIMPER (**10**). According to this investigator the archegonium, arising directly from the apical cell of a branch, begins its development by an apical cell with two cutting faces, just as in the true mosses, and forms in this manner about 6 cells. The events that follow, being beyond the technique of that time, are described in a hazy manner and may be passed over here. Paraphyses are said to occur among the archegonia.

The brief account given by HOFMEISTER (**5**) does not differ from that of SCHIMPER.

In 1869 LEITGEB (**8**), while working out the development of the antheridium, found a few female branches, and on each, one archegonium was being formed, arising directly from the apical cell of the branch, but whether the divergence of the division walls is one-half, as HOFMEISTER and SCHIMPER thought, or whether, as in the antheridium, there are smaller divergences, and furthermore from what cells the secondary archegonia arise, he is unable to say because of a lack of material.

The account given by JANCZEWSKI (**7**) in 1872 may be summarized as follows. The apical cell elongates and is divided by

cross-walls, finally consisting of 3 or 4 cylindrical cells, each of which makes secondary divisions, and above these two cells whose walls are obliquely placed and which also make secondary divisions. The origin of the archegonium proper and the formation of adventitious segments and canal initials are declared to be the same as among the mosses. In *Sphagnum rigidum* and *S. acutifolium* "anomalies" in the development are reported, though the regular process described above also occurs. No explanation is offered as to what these "anomalies" are. It is to be regretted that no illustrations accompany the article.

The most recent account is that given by GAYET (3) in 1897. He agrees with LEITGEB that the first archegonium is axillary, but dismisses the early stages with the brief statement that "the first divisions are normal." The two figures given to illustrate this are by no means clear, so that one is left in doubt as to the meaning of the word normal. GAYET is unable to find the two cells with oblique walls reported by JANCZEWSKI and thinks them an error of interpretation. The neck of the archegonium is said to elongate by the division of the terminal cell, and this terminal growth is produced without giving rise to canal cells.

From these brief reviews it is evident that there is little agreement among investigators as to developmental processes, and that the whole subject is in a haze of uncertainty.

EARLY STAGES IN THE DEVELOPMENT OF THE ARCHEGONIUM

In the autumn, at the time of the production of sex organs, the elongation of the main axis is checked, so that the newly formed branches whose apical cells are being transformed into archegonia appear as a cluster or bud about the main axis at the apex. This transformation of the apical cells of the side branches into archegonia is not simultaneous, but proceeds acropetally, occurring earlier and earlier in the development of each branch as one passes toward the apex. As yet this transformation process has not been observed to reach the apical cell of the main stem, though more than 400 slides bearing on this point have been examined.

In the material studied the maximum number of archegonia arising from an apical cell is three. In such a case each of the

two segments last formed becomes the initial of a secondary archegonium, while that portion of the apical cell above and not included by them is the initial of the primary archegonium (fig. 2). Fig. 3 shows this in cross-section. A few examples have been noted where one of the secondary segments, after making several divisions, has for some reason been checked and remains as a slight projection on the base of the mature primary archegonium. In some cases only the last formed segment develops as a secondary archegonium; while still more rarely no secondary archegonia are formed at all, the apical cell becoming the initial of a single archegonium (fig. 5).

THE PRIMARY ARCHEGONIUM

The primary archegonium shows a remarkable variation in the manner of its early divisions. The first wall may be transverse (fig. 6) or slanting (fig. 4). If the first wall is slanting, the second may be transverse (fig. 5). However, by the examination of a large number of slides one may recognize two general types of development. A filament of cells, usually 4 or 5 in number, may be formed by successive transverse divisions of the apical cell (figs. 6–9). Four or five cells may be produced by the activity of an apical cell with two cutting faces (figs. 11, 12); this is probably the most frequent method. Between these two extremes there may be various mixtures of planes. An interesting intermediate condition in which the walls do not quite intersect is shown in figs. 10 and 13.

At this point the question may be asked, Why are not figs. 6–9 merely the development of an apical cell with two cutting faces seen at an angle of 90° from the plane represented by figs. 11 and 12? This matter has been carefully examined and the following facts presented as an answer. Unquestionably the walls may have such an appearance, but the test is their behavior under the oil immersion lens. If the walls are transverse, they remain steady on focusing up and down; but if of the kind formed by an apical cell with two cutting faces, they swing in a characteristic manner as one changes the focus. Frequent examples of this have been found, as well as those in which there was no shifting.

Hence figs. 6–9, belonging to this latter class, are known to be transverse.

THE SECONDARY ARCHEGONIUM

The secondary archegonium shows a greater degree of uniformity. The initial divides into an inner and an outer cell (figs. 6, 10). This outer cell by subsequent transverse divisions (figs. 8, 9, 14) gives rise to a filament of cells, 5 or 6 in number, in each of which the usual secondary divisions occur (fig. 16*b*). As yet no evidence has been found that the secondary archegonium may develop by an apical cell with two cutting faces.

THE DEVELOPMENT OF THE ARCHEGONIUM PROPER

After there has been formed, as described above, a filament of cells by transverse walls, or a series of cells by an apical cell with two cutting faces, and secondary divisions have occurred in each segment except the terminal one, the development of the archegonium proper begins in the manner usual among the Bryophytes. In the terminal cell, which becomes somewhat enlarged, three oblique walls appear, cutting off three peripheral segments and originating a large cell within, which has the form of an inverted truncated pyramid (figs. 13, 14). This large cell we shall designate the primary axial cell. On division it gives rise to an outer axial cell, the cover cell, and an inner axial cell, the central cell (figs. 17–19). The wall cells of the archegonium arise from the three peripheral segments.

Up to this point the development of the archegonium proper coincides exactly with the description given by numerous investigators for the archegonium of the Bryophytes, whether Hepaticae or Musci. It is in the events immediately following that there is a divergence of views and theories. For the sake of continuity we shall postpone the presentation of these theories until later and continue the description of the developmental processes.

Here then the important question arises, What is the part played by the cover cell and what by the central cell in the further development of the archegonium? The answer must be found in a study of sections both longitudinal and transverse.

THE COVER CELL

Figs. 18 and 19 represent typical cases in the appearance of the archegonium with cover cell and central cell formed. It will be noted that the two cover cells differ in size. This is due to the peculiar shape of the cover cell, coupled with the direction of the cut. In fig. 18 the cut is median through the long diameter; in fig. 19 through a shorter diameter. This may be more clearly understood by an examination of the cover cells as shown in transverse sections (figs. 53–55).

It is important to note that the cover cell may divide by a vertical wall into two almost equal segments before the division of the central cell takes place (figs. 21, 54). But more important still is the evidence that by the time the central cell has completed its division into primary neck canal cell and primary ventral cell, the cover cell has at least become divided by a vertical wall into two almost equal segments (figs. 22, 24), and in some cases has formed a quadrant of cells (figs. 23, 56). The division lines between the cells of the cover and the outer cells of the neck are clearly marked and easy to follow in the younger stages. Thus in figs. 29–32 the cover is literally the cap of the archegonium, and in each case contains 6 cells (three each in median longitudinal section, as illustrated). In fig. 33 the cover consists of 8 cells. However, in the older stages the cells of the cover and the neck usually merge so insensibly that the two cannot be separated with any degree of certainty. Hence no accurate statement as to the final number of cells produced by the cover can be made.

From the foregoing facts it is evident that the cover cell divides early by a vertical wall into two almost equal segments. Subsequent vertical divisions in each of these segments produce a plate of cells, 8 or more in number, which covers the apex of the archegonium and in mature forms merges insensibly with the upper cells of the neck. There is not the slightest evidence to show that the cover cell cuts off any basal segments.

THE CENTRAL CELL

The division of the central cell into primary neck canal cell and primary ventral cell is shown in figs. 20 and 21. The primary

neck canal cell is the mother cell of the neck canal row. The spindle for the division into two canal cells, as shown in fig. 25, has been found four times in the material studied. From this point on the cells of the canal row divide in almost any order. The evidence for this shown by the spindles in figs. 27, 28, 30, 31, and 34. By this intercalary growth a row of canal cells, usually 8 or 9 in number, is formed (figs. 38, 40).

The division of the primary ventral cell occurs late. Fig. 38 shows 8 canal cells and the ventral cell undivided; while we were fortunate enough to find a spindle when there were 7 canal cells (fig. 39). The ventral canal nucleus produced by this division is peculiar, being only a trifle smaller than the egg, and is remarkable in that it is regularly persistent and behaves for a time just as does the egg. Not long after the division into ventral canal cell and egg, the canal row begins to disintegrate (this process having a variable beginning, through quite often acropetal), but not so the ventral canal cell. Its cytoplasm begins to condense about the nucleus (the same process occurring about the egg), and soon we have in a mature archegonium the appearance of two eggs separated by a wall (fig. 41). Later the cytoplasm about each of these two nuclei becomes markedly condensed and rounded off and may be easily observed in the living material. Still later the wall between the two cells breaks down and the nuclei, each as the center of a ball of cytoplasm, come to lie near together in the venter of the archegonium. Usually just before fertilization the ventral canal nucleus disintegrates.

THE GROWTH OF THE ARCHEGONIUM

We have already shown that the growth of the canal row is intercalary. The same is true of the growth of the wall cells. Fig. 26 gives valuable evidence on this point. It is not an exceptional case, but was found a number of times. The evidence goes to show that about the stage of two canal cells there comes a sudden vigorous growth of the archegonium through intercalary divisions, this process frequently involving one or two rows of cells simultaneously. This sometimes results in one side of the archegonium becoming longer than the other, tilting the cover, as is shown in

figs. 33–35. In the older stages the growth is slower, but spindles in various cells of the periphery give further undoubted evidence of intercalary growth.

THE MATURE ARCHEGONIUM

In the account of the development of the archegonium given by the various authors already mentioned there has been much discussion concerning the mature archegonium. It will be of interest, therefore, to record the facts in regard to *S. subsecundum*. The archegonia here may be divided into two classes or types, those long and slender and those massive. This difference begins to appear early and may be clearly seen by a comparison of figs. 30 and 32 or 34 and 35. Naturally, therefore, we find variability in the mature stages. In its simplest portion, the neck for a short distance may have 6 rows of cells, or in the more massive types each cell of the 6 rows may have one or more secondary divisions. Fig. 58 represents a typical series through the simplest portion of such a neck. The neck merges gradually into the venter, which is usually 4 cells thick (fig. 59), though simpler venters may also be found.

ABNORMALITIES

Abnormalities are of rather frequent occurrence in *S. subsecundum*. Double venters (fig. 42), unequal division of the venter, the ventral canal nucleus larger than the egg (fig. 43), ventral canal nucleus the same size as the egg (fig. 44), and multiple eggs (fig. 45) are not of rare occurrence.

THE ABSENCE OF PARAPHYSES

SCHIMPER (**10**) in his elaborate monograph reports structures among both antheridia and archegonia which he calls paraphyses. Other investigators have been unable to find any trace of paraphyses. We have taken particular pains to investigate this in *S. subsecundum*, dissecting hundreds of heads, both antheridial and archegonial, but not the slightest indications of paraphyses could be found. This was further confirmed by an examination of about 500 slides with the same result. In a few cases the branched hyphae of a fungus, *Tilletia Sphagni*, were observed

about some of the archegonia. This, as has already been suggested by several investigators, may account for the so-called paraphyses of SCHIMPER. We feel safe, therefore, in stating that so far as *S. subsecundum* is concerned there are no paraphyses about either the antheridia or the archegonia.

THE MUCILAGE HAIRS

The peculiar structures developing in the axil of each young leaf have been commented on by several investigators. A complete series in the development may be easily followed out. One of the axillary cells at the base of the leaf becomes papillate (fig. 47), divides into an upper cell and a basal cell (fig. 49), and the upper cell makes two acropetal divisions resulting in a filament of three cells (figs. 49, 50). This is the mature stage. The terminal cell of the filament usually becomes enlarged and is filled with a dark staining substance, probably mucilage. Several mucilage hairs may arise from the axillary row at the base of a leaf (fig. 49). Occasionally branched forms may be found (fig. 51). As the leaf grows older the hairs disappear.

Discussion

So far as the young stages in the development on the archegonium are concerned, it appears that HOFMEISTER (**5**), SCHIMPER (**10**), and JANCZEWSKI (**7**) are all correct. An examination of many sections shows development by all the methods reported, as well as intermediate conditions not reported. In the development of the archegonium proper we are unable to find any evidence to support the statement of JANCZEWSKI (**7**) that adventitious segments and canal initials are cut off as in the Musci. Furthermore, the evidence is clear and emphatic that the growth of the archegonium is not terminal, as GAYET (**3**) holds, but is intercalary. The spindles shown in various figures are conclusive on this point.

We must now consider briefly the theories of archegonial development among the Bryophytes, and the natural question as to what bearing this investigation has upon these theories.

JANCZEWSKI (**7**), GOEBEL (**4**), CAMPBELL (**1**), HOLFERTY (**6**), and others hold that the archegonium of the Musci is to be distin-

guished from that of the Hepaticae by its peculiar apical growth; that in the Musci the canal cells do not arise by the activity of one mother cell as in the Hepaticae, but are produced in part by the division of the cover cell. This cover cell cuts off two sets of segments, the one being parallel to the axis of the archegonium and forming the wall cells of the neck; the other parallel to the base of the archegonium and contributing to the neck canal row.

The view presented by GAYET (3) is in the main a contradiction. He holds that in both Hepaticae and Musci the growth of the archegonium is terminal, but no internal segments are added to the canal row by the cover cell, which cuts off segments forming the wall cells of the neck.

SERVETTAZ (9, pp. 169–171) in a recent paper has advanced a new interpretation of archegonial formation. His description of the development in *Phascum cuspidatum* may be summarized as follows. The initial cell divides transversely and gives a basal cell and a superior cell. The superior cell then divides obliquely a certain number of times, from two to five; then one of the cells placed below the terminal cell divides tangentially and determines the formation of a central cell, which by basipetal divisions gives a row of 8 cells, the canal row, the ventral canal cell, and the egg. The evidence offered for these statements certainly is not convincing, and if true this origin of the central cell differentiates *Phascum* from any of the Bryophytes now known.

The evidence we have presented for *Sphagnum* has nothing in it to support the views of SERVETTAZ (9) and GAYET (3). Furthermore, it breaks the distinction between Musci and Hepaticae drawn by JANCZEWSKI (7), CAMPBELL (1), GOEBEL (4), etc. Here at least is one of the Musci in which the cover cell does not add to the canal row.

Conclusions

The archegonium of *Sphagnum subsecundum* is synthetic. The stalk, the thick venter, and the comparatively slender twisted neck are moss characters; the relatively inactive cover cell, the intercalary growth of the archegonium, and the low number of canal cells are hepatic characters as we know them today.

Summary

1. During the autumns of 1912 and 1913 sex organs have been found in vast numbers on *Sphagnum subsecundum* in the vicinity of Mineral Springs, Indiana.

2. On approaching maturity the archegonial heads may be recognized by the colored bud in the center of the head at the apex. Analysis of the bud shows terminal archegonia on short side branches.

3. The archegonia begin to develop in September.

4. The apical cell of a side branch is a primordium; each of the two segments last formed becomes the initial of a secondary archegonium, while that part of the apical cell above and not included by these segments is the initial of the primary archegonium.

5. There is great irregularity in the early stages of the development of the primary archegonium: there may be a filament of cells by the successive transverse divisions of the apical cell; or growth by an apical cell with two cutting faces; or a mixture of planes.

6. As yet the secondary archegonium has been found to develop only by the successive transverse divisions of the apical cell.

7. The archegonium proper is initiated in the manner usual among the Bryophytes. In the terminal cells three oblique walls cut off three peripheral segments and originate the primary axial cell within, which on division gives rise to cover cell and central cell.

8. The cover cell is relatively inactive and cuts off no basal segments.

9. The central cell on division forms the primary neck canal cell (the mother cell of the neck canal row) and the primary ventral cell.

10. The growth of the neck canal row is intercalary, the cells dividing in almost any order.

11. The primary ventral cell divides late into ventral canal cell and egg.

12. The growth of the wall cells of the archegonium is intercalary.

13. The mature archegonium has 8 or 9 canal cells.

14. The breaking down of the canal row may begin at any point, is frequently acropetal, but never involves the ventral canal cell.

15. The ventral canal cell is persistent, behaves for a time exactly as does the egg, but normally disintegrates just before the archegonium opens for fertilization.

16. Abnormalities, such as double venters, multiple eggs, etc., are of common occurrence.

17. The archegonium of *Sphagnum* is synthetic, combining certain characters of the Hepaticae with others of the Musci.

The author wishes to express his sincere thanks to Professor JOHN M. COULTER and Dr. W. J. G. LAND for helpful advice and discussion; and to Mr. E. J. HILL who kindly identified the material studied.

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EXPLANATION OF PLATES IV–VII

All figures were drawn with aid of Abbé camera lucida at table level, and, being reduced one-half in reproduction, now show the following magnifications: figs. 1–35, 43–56, ×525; figs. 36–42, 57, ×300; figs. 58–59, ×180.

Abbreviations are as follows: *a*, primary archegonium or its initial; *b*, *c*, secondary archegonia or their initials; *l*, leaf.

PLATE IV

FIG. 1.—Primordium showing a primary initial and one secondary initial.

FIG. 2.—Tangential section through primordium, showing primary initial and two secondary.

FIG. 3.—Same in transverse section; dotted line shows plane of cut in fig. 2.

FIG. 4.—First wall in primary initial slanting; secondary initial has divided to form an inner and an outer cell.

FIG. 5.—First wall in archegonium initial slanting, second transverse; no secondary formed.

FIG. 6.—First wall of primary initial transverse.

FIG. 7.—Uppermost wall of primary initial transverse; next below tilts slightly; secondary not shown.

FIG. 8.—Two transverse walls in primary archegonium; secondary shows first transverse wall.

FIG. 9.—Three uppermost stories of primary archegonium formed by transverse walls.

FIG. 10.—Walls of primary archegonium do not quite intersect.

FIG. 11.—Development of the primary archegonium by an apical cell with two cutting faces; first transverse wall has appeared in the secondary archegonium.

FIG. 12.—The same, slightly older.

FIG. 13.—Stalk of archegonium formed chiefly by walls that do not intersect; in terminal story the primary axial cell has been originated by the three oblique walls.

FIG. 14.—Stalk of primary archegonium regular; primary axial cell cut out; median longitudinal section through secondary archegonium showing two transverse walls.

FIG. 15.—Tangential section through secondary archegonium showing two transverse walls.

FIG. 16.—Group consisting of primary archegonium and two secondary; the primary and one secondary shown in outline.

FIG. 17.—Division of primary axial cell into cover cell and central cell.

FIG. 18.—Cover cell and central cell.

FIG. 19.—The same.

FIG. 20.—Division of central cell into primary neck canal cell and primary ventral cell.

FIG. 21.—The same, but shows cover cell divided.

FIG. 22.—Primary neck canal cell and primary ventral cell formed; cover cell has divided into two almost equal segments; plastids beginning to be conspicuous about each nucleus.

FIG. 23.—The same, but cover is forming a quadrant; the cell on the left shows a figure, while that on the right has divided in the same plane.

PLATE V

FIG. 24.—Primary neck canal cell and primary ventral cell; unequal growth in the walls pushing cover to one side.

FIG. 25.—Primary neck canal cell in division.

FIG. 26.—Two neck canal cells and the primary ventral cell; intercalary growth in the walls of the archegonium, pushing cover to one side; plastids becoming conspicuous.

FIG. 27.—Slender type of archegonium with two neck canal cells and the primary ventral cell; the uppermost neck canal cell is in division.

FIG. 28.—Simultaneous division of the two neck canal cells.

FIG. 29.—Three neck canal cells and primary ventral cell; cover has 6 cells (three shown in median longitudinal section).

FIG. 30.—Slender type of archegonium with three neck canal cells and primary ventral cell; figure in terminal neck canal cell; cover as above.

FIG. 31.—Three neck canal cells and primary ventral cell with figure in basal neck canal cell; cover as above.

FIG. 32.—Massive type of archegonium; four neck canal cells and primary ventral cell; cover as above.

FIG. 33.—Five neck canal cells and primary ventral cell; cover, tilted to one side, has 8 cells (4 shown).

FIG. 34.—Five neck canal cells and primary ventral cell; the middle neck canal cell is in division.

FIG. 35.—Six canal cells and primary ventral cell; cover, irregular through disturbance, has 8 cells; plastids conspicuous in the canal row.

FIG. 36.—Symmetrical type of archegonium, having 6 neck canal cells and primary ventral cell; cover difficult to follow, but probably has 8 cells (4 shown).

FIG. 37.—Seven neck canal cells and primary ventral cell.

PLATE VI

FIG. 38.—Eight neck canal cells and primary ventral cell.

FIG. 39.—Seven neck canal cells and primary ventral cell in division to form ventral canal cell and egg.

FIG. 40.—Nine neck canal cells, ventral canal cell, and egg.

FIG. 41.—Neck canal cells broken down; protoplasm beginning to round off about ventral canal nucleus and egg.

FIG. 42.—Fine example of double venter.

FIG. 43.—Unequal division; ventral canal nucleus larger than egg.

FIG. 44.—Elongated venter almost equally divided; ventral canal nucleus same size as egg.

FIG. 45.—Venter with 4 cells; the 3 lowest probably are eggs, the uppermost the ventral canal cell.

FIG. 46.—Median longitudinal section through cap of mature archegonium, showing unusual divisions.

FIG. 47.—Section tangential to face of leaf; first stage in the development of mucilage hair; axillary cell at base of leaf becomes papillate.

FIG. 48.—Nucleus has divided and papillate cell cut off by a wall.

FIG. 49.—Acropetal division of the papillate cell.

FIG. 50.—Second acropetal division of the papillate cell; the mature mucilage hair.

FIG. 51.—Branched form of mucilage hair.

PLATE VII

FIG. 52.—Series of transverse sections through young primary archegonium and two secondary.

FIG. 53.—Serial sections through archegonium proper, showing cover cell and central cell.

FIG. 54.—Serial sections; the cover cell has divided, but central cell is yet undivided.

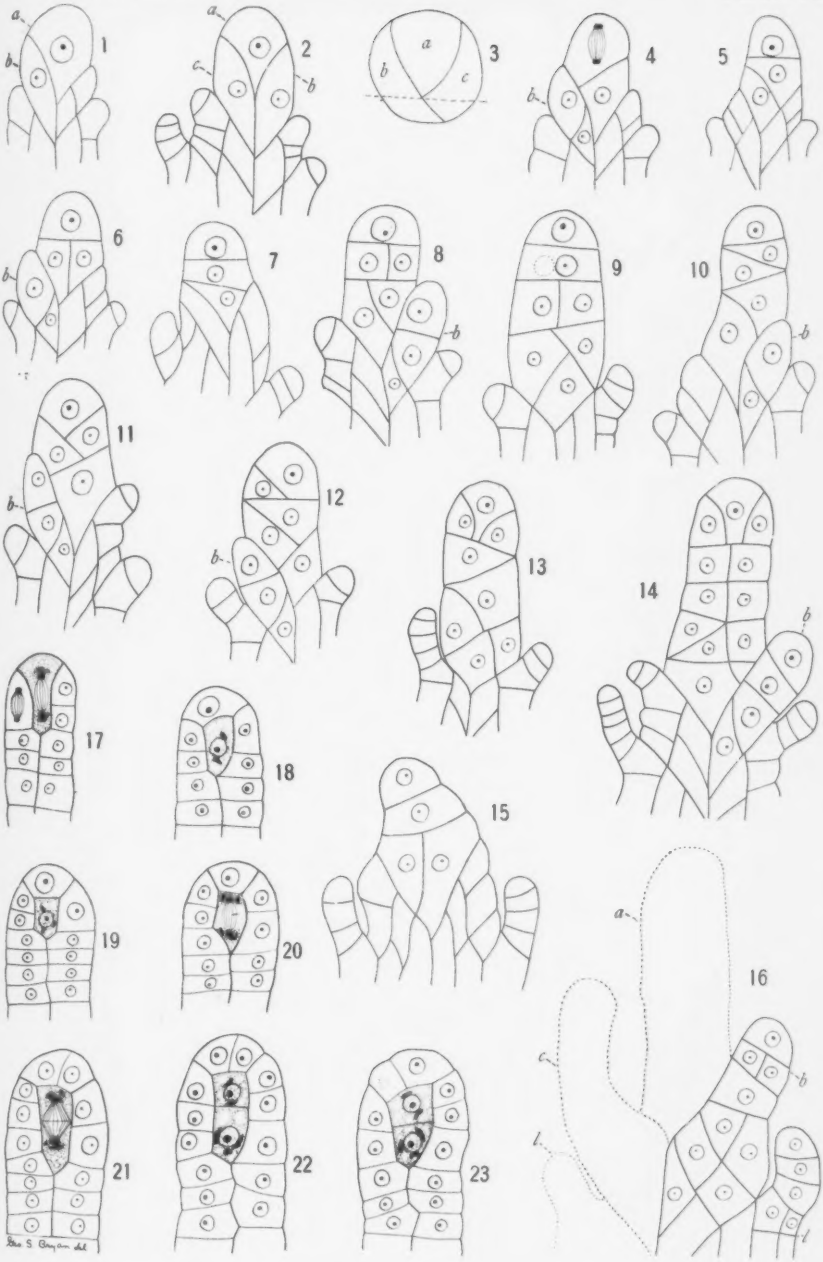
FIG. 55.—Serial sections, showing in the formation of the archegonium proper the three oblique walls which have cut off the peripheral segments and originated the primary axial cell within.

FIG. 56.—Serial sections through archegonium having primary neck canal cell and primary ventral cell; the cover cell has formed a quadrant of cells.

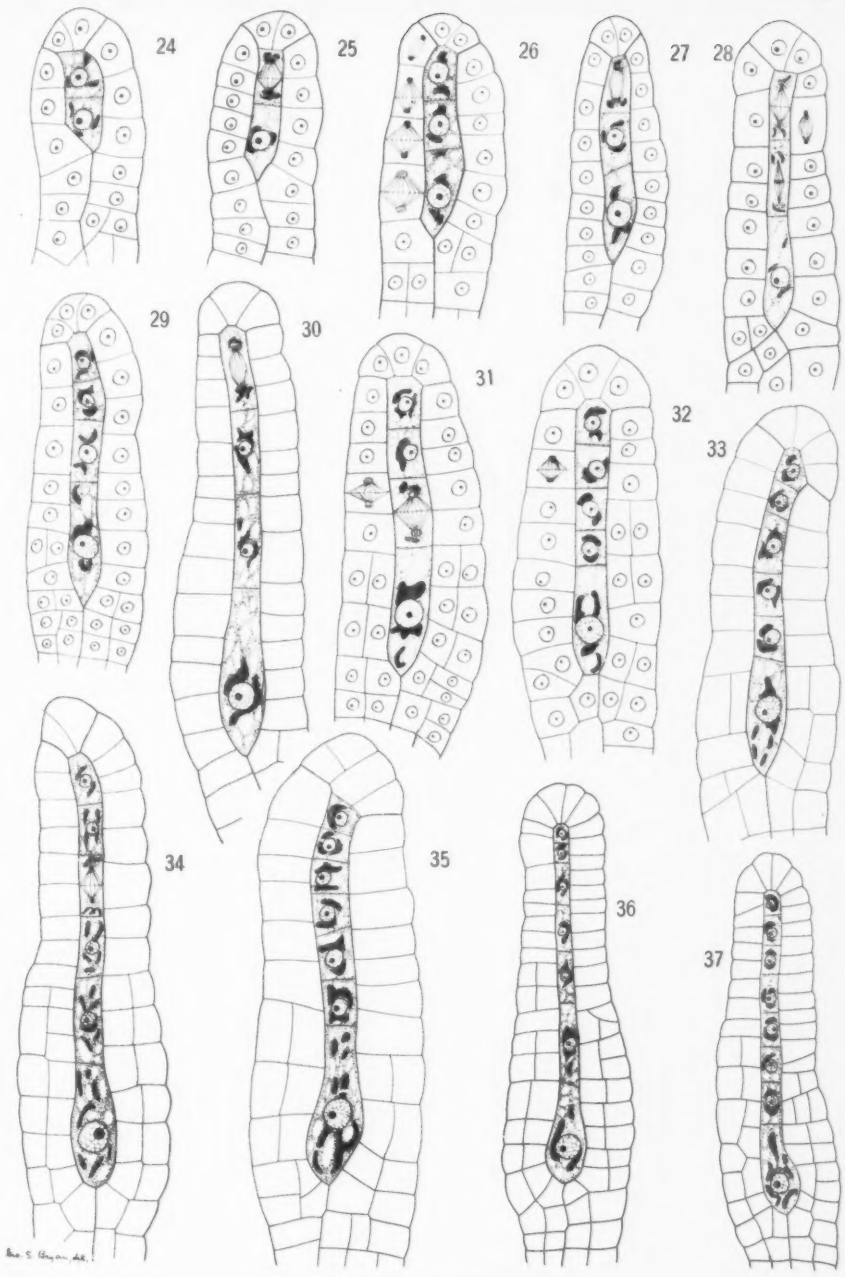
FIG. 57.—Serial sections through archegonium with 6 canal cells and ventral cell; the cover contains 8 cells; the gradual transition from cap to neck to venter is well shown.

FIG. 58.—Serial sections through simplest portion of neck of mature massive type of archegonium; section *A* shows the characteristic thickenings toward the cap.

FIG. 59.—Venter of same series at level of egg nucleus.



BRYAN on SPHAGNUM



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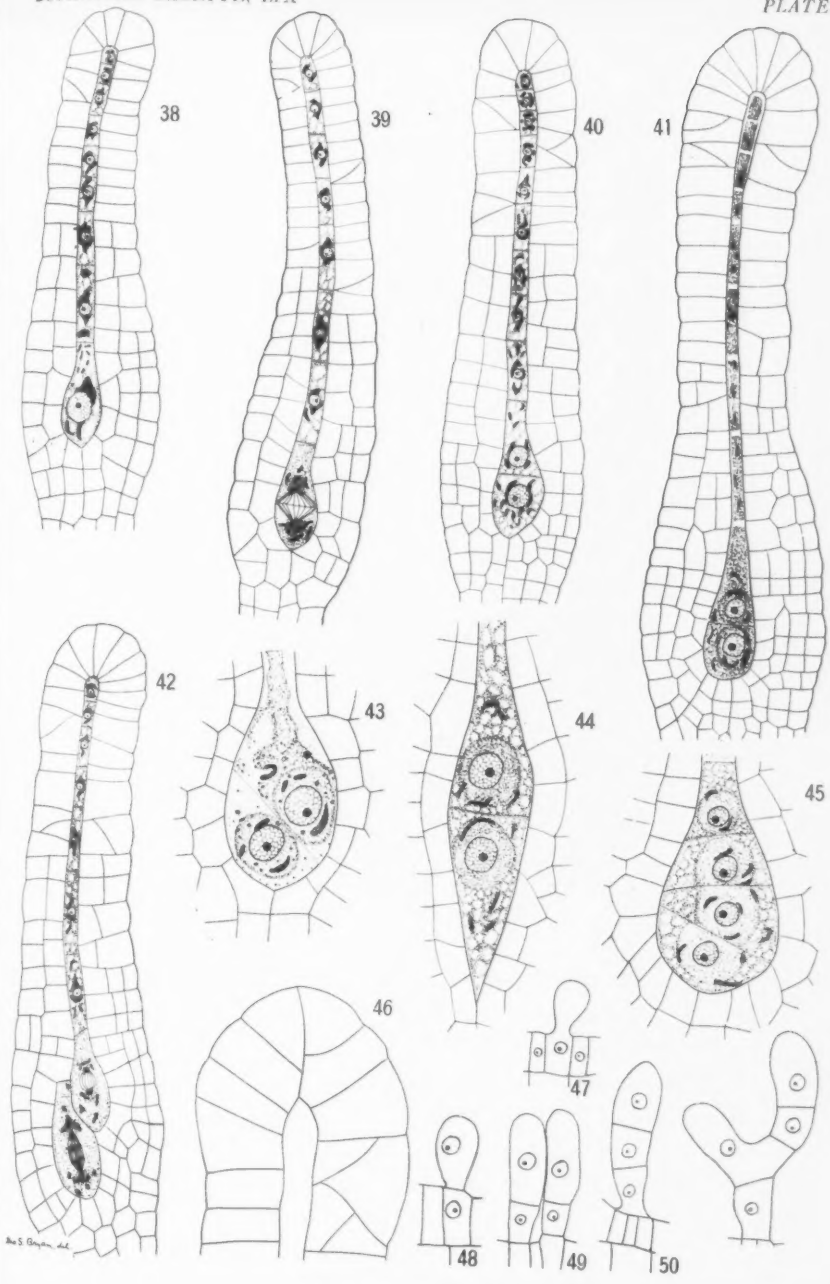

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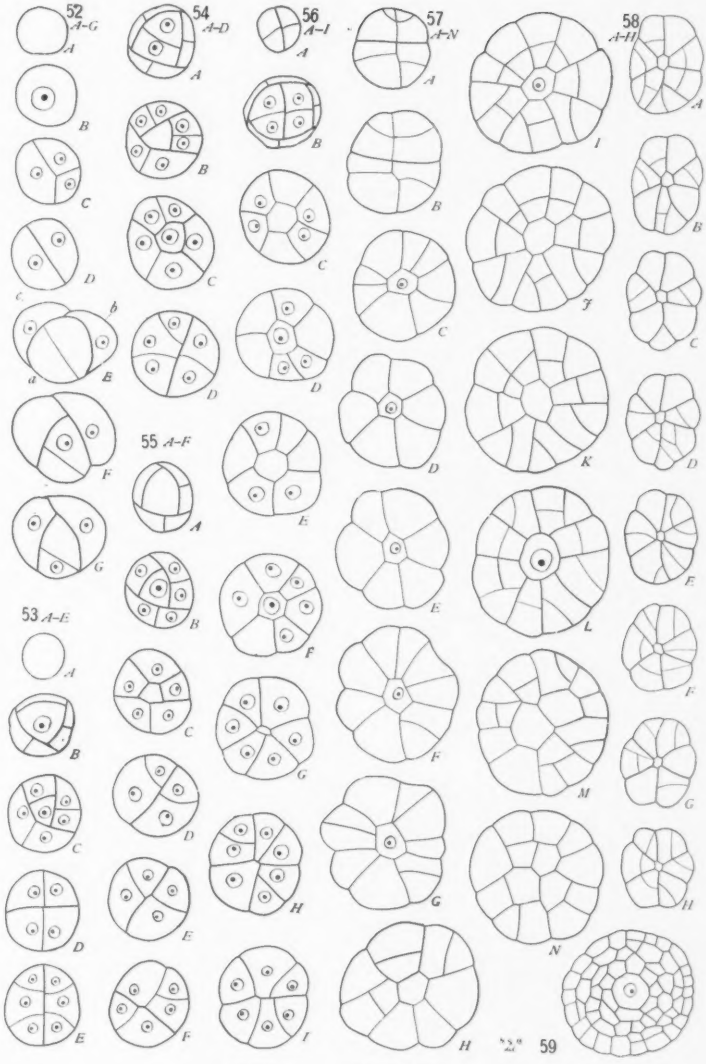

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CURRENT LITERATURE

BOOK REVIEWS

Plant physiology

The third German edition of JOST'S *Lectures on plant physiology*[1] shows certain changes from the first edition in general organization and point of view. Instead of the headings "Stoffwechsel," "Formwechsel," and "Energiewechsel," for the general divisions of the subject, the new edition has "Stoffwechsel," "Formwechsel," and "Ortwechsel." The heading "Energiewechsel" is used for chap. xix, the last chapter under "Stoffwechsel." This brings the energy transformations into close connection with the source of the energy, which is quite desirable in contrast with the attempt to connect it with any particular manifestation of energy, as movement. Lecture 17 of the new edition has the heading "Oxidation of hydrogen sulfid, hydrogen, methane, and ammonia by bacteria. Carbon assimilation without light and chlorophyll." It corresponds to lecture 18 of the first edition with the heading "Sulfo and nitro bacteria." Several other changes appear in lecture headings, indicative of change in viewpoint or content. The introductory lecture to "Formwechsel" has been cut down to five introductory paragraphs in the chapter on "Growth of the cell." The 43 lectures of the first edition thus become 42 in the present edition, but the pages have increased from 695 to 760.

As one reads this excellent treatise, he is impressed by the number of subjects of which the author has an excellent critical grasp; plant physiology, plant anatomy, evolution and heredity, physiological chemistry, etc. JOST has a genius for organization and is apparently a natural teacher free from pet theories or hobbies. One is inclined to compare him, as a teacher and organizer of the subject, with SACHS, remembering, however, that the task of organizing the subject is now far more difficult, owing to the enormous amount of experimentation and range of knowledge to be included. In most parts of the treatise there are excellent summaries of the subjects, entirely up to date. This is illustrated by the statement on the synthesis of amino acids, lecithin, proteins, etc., which embodies the late work of TRIER and others; by the greatly improved statement on catalysis and enzyme action; and by the lectures on hybridization and heredity, on variation, and on species-formation.

[1] JOST, LUDWIG, Vorlesungen über Pflanzenphysiologie. xvi+760. *figs. 194.* Jena: Gustav Fischer. 1913.

The reviewer believes that JOST's treatment of transpiration could be greatly improved by adopting LIVINGSTON's idea and method of relative transpiration. This gives quantitative determination of the inhibitory and regulating factors at work in the leaf under various conditions. The very exact work of BRIGGS and SHANTZ on wilting coefficient is passed over with mere citation, and data obtained from the rather indefinite work of SACHS on non-available water.

Many will believe that JOST's meager and derogatory statement of the place of colloids in plant physiology is very inadequate and faces away from future progress in the subject. The statement on dormancy in seeds could have been written twenty years ago as well as now. JOST apparently attempts to illuminate the simple by the complex when he likens the temperature curve for rate of diastatic action to similar curves for protoplasmic activity. It would be very much more to the point to explain that we know very largely the chemistry and physics of the first curve. Rise of temperature increases the rate of diastatic action with a rather constant coefficient (somewhat less than 2 for each 10° rise). It also increases the rate of coagulation of the enzyme, especially rapidly at higher temperatures, hence the high optimum. The coagulation is a function of the time as well as of the temperature. This accounts for the optimum being much lower when the duration of the experiment is great. The failure of JOST to apply the idea of time as a factor in coagulation of proteins by heat is evident a number of times in the book, especially in his dismissal of LEPESCHKIN's conclusion that death in general from supramaximal temperatures is due to the coagulation of cell proteins. While at one point JOST accepts and clearly discusses BLACKMAN'S conclusions on "optima and limiting factors," he frequently lapses into the older German view and phraseology. JOST's arguments in favor of the claim that rate of water absorption by a cell as affected by temperature is a matter of protoplasmic regulation are rather weakened by the recent work of BROWN and WORLEY on barley grains, in which they found that temperature effects appear with about the same coefficient when non-living membranes only or chiefly are involved. Many of these criticisms are an outgrowth of JOST's peculiar brand of vitalism. If he is convinced beyond a doubt that a physical or chemical explanation holds, he accepts it, but at too many points in his lectures he fails to outline the attack along these lines.

In spite of its virtues in organization, the book could be greatly improved by better organization of the materials within the chapters and by a far more extensive index. At many points the author makes extensive detours from the subject under discussion. Graduate students frequently complain that they must read certain lectures several times and finally reorganize them before they can be held in mind. Paragraph headings such as BARNES or NATHANSOHN have used would serve the double purpose of making the plan of organization more evident and perhaps of leading to a better plan. An author index separate from or as a part of a more extensive general

index would render the material of the book more accessible.—WILLIAM CROCKER.

Biochemistry of plants

In revision, the first volume of CZAPEK's *Biochemistry of plants*[2] has grown from 584 pages to 828 pages. The historical introduction contains 18 pages as in the previous edition. The portion on "general biochemistry" contains 220 pages as compared with 77 pages in the old edition. Under "special biochemistry" the first part ("The sugars in the metabolism of plants") has been increased from 397 pages to 469; and the second part ("The lipoids in the metabolism of plants") has grown from 94 pages to 112. One of the most notable changes in the general organization of the book is the treatment of the lipoids after the sugars instead of before. This seems desirable because of the order of synthesis of the two groups of substances in the plant.

The "general biochemistry" contains the two chapters of the old edition, "The substratum of the chemical processes in the living organism" and "Chemical reactions in the living plant organism," with two additional chapters entitled "Chemical stimulation effects" and "The chemistry of adaptation and heredity." In this part one is impressed with the excellent summary of the literature on general characters of colloids, gels and adsorption phenomena, catalysis, general chemistry of enzymes, and kinetics of enzyme action.

The part on sugars in the metabolism of plants shows few changes in organization. The additional space used is largely due to the growth of the literature of the subject.

The part on lipoids is divided into two sections, "The nutrient lipoids of the plant" and "The cytolipoids of plants." In the first section, the chapter headings are identical with those of the first edition: "The reserve fats of seeds," "Resorption of fats in seed germination," "Fat synthesis in ripening seeds and fruits," "Reserve fats in stems and leaves," "Reserve fats in thallophytes, mosses, ferns, and pollen grains." The section on cytolipoids has undergone some changes in organization and more in content. The chapter headings are "Plant cerobrosides," "Sterinolipoids of plants (phytosterol and related bodies)," "Plant chromolipoids," and "The production of wax."

The table of contents has been greatly improved by the addition of heads and subheads, giving a much better grouping of the chapters. The treatment of such subjects as photosynthesis, alcoholic fermentation, respiration, and other plant processes reminds one that the work is by no means a plant chemistry in the narrow sense of the word. It is more nearly a physiology of metabolism in plants, with main emphasis on the fundamental chemistry and physics involved in the processes.—WILLIAM CROCKER.

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[2] CZAPEK, FR., Biochemie der Pflanzen. 2d ed. Vol. I. pp. xix+928. Jena: Gustav Fischer. 1913.

Physiological plant anatomy

An English translation of the fourth edition of HABERLANDT'S *Physiologische Pflanzenanatomie*[3] will be welcomed by all who have been engaged in the study and teaching of this particular phase of the science, particularly as it will make the investigations of this leader in physiological anatomy more readily available for students. As pointed out by the translator, the latest German edition, recently reviewed in this journal,[4] may be assumed to embody the mature and considered views of its author with regard to this section of botanical science. In the chapter on sense organs, in particular, there is much original data, now appearing for the first time in English. Here no one will question the facts presented, although many will object to the teleological interpretations given by HABERLANDT.

The translator seems to have done his work very well, at times using considerable freedom to obtain a desirable clearness of expression quite in keeping with the meaning of the original. The volume is well printed in a most legible type, and all the illustrations, notes, and bibliography of the German edition are retained. One might sometimes wish, however, for complete citations of the literature.—GEO. D. FULLER.

MINOR NOTICES

A northwestern manual.—FRYE and RIGG[5] have prepared a manual for the use of schools of Oregon, Idaho, Washington, and the coastal region of southwestern British Columbia. These special manuals for relatively restricted regions are very useful for schools, since the keys can be made much more direct and simple, and the descriptions can be fitted more closely to the local conditions than is possible in manuals that cover a large area. The book is well organized, with every device for easy use, and should prove well adapted to its purpose. The real test of a manual lies in its use, and the reviewer cannot estimate this one from such a standpoint, but he has every reason to believe that the long experience of the authors in the region covered has enabled them to fit the work exactly to its purpose.—J. M. C.

Plantae Wilsonianae.—SARGENT[6] in co-operation with several specialists has recently issued, as a fourth part of *Plantae Wilsonianae*, another important

[3] HABERLANDT, G., Physiological plant anatomy, translated from the 4th German edition by Montagu Drummond. 8vo. xv+777. *figs. 291*. London: Macmillan. 1914. $6.50.

[4] BOT. GAZ. **55**:402. 1913.

[5] FRYE, T. C., and RIGG, G. B., Elementary flora of the Northwest. pp. 256. New York, Cincinnati, and Chicago: American Book Co. 1914.

[6] SARGENT, CHARLES SPRAGUE, Plantae Wilsonianae. An enumeration of the woody plants collected in western China for the Arnold Arboretum of Harvard University during the years 1907, 1908, and 1910 by E. H. WILSON. Part IV. Publications of the Arnold Arboretum. no. 4, 8vo. pp. 262. Cambridge: The University Press. Issued March 24, 1914.

contribution to our knowledge of the flora of China. The present part, like the preceding ones, is based primarily on a critical study of plants collected in western China by E. H. WILSON, but it includes also citations of collections made by HENRY, FAURIE, JACK, PURDOM, SARGENT, TAQUET, and others. Upward of 100 species and varieties new to science are recorded in some 40 different genera. The importance of the work lies, not only in the record of new plants, but also in the incorporation of much synonomy and bibliography from scattered publications.—J. M. GREENMAN.

NOTES FOR STUDENTS

Hereditary symbiosis.—One of the most remarkable of recent botanical discoveries, that of hereditary symbiosis between bacteria and seed plants, was made independently by MIEHE and VON FABER,[7] thus adding another to the notable list of great simultaneous achievements. As early as 1894 TRIMEN noted the persistent presence of small knotlike excrescences on the leaves of certain tropical Rubiaceae of Ceylon. In 1902 ZIMMERMANN noted the constant presence of bacteria in these structures, at least in four species from Java, whereupon he referred to them as bacterial knots (*Bacterienknoten*). Since ZIMMERMANN did not take up the question of the origin of the bacterial knots, VON FABER went to Buitenzorg in 1910 to make an extended study of them. A preliminary report of his early observations was made in 1911, and a full account followed in 1912.[8]

VON FABER investigated the symbiotic relations of five species of Rubiaceae, viz., *Pavetta indica*, *P. angustifolia*, *P. lanceolata*, *P. Zimmermanniana*, and *Psychotria bacteriophila*. In the closed buds the bacteria are found in resinous masses in among the leaf primordia. As the leaves develop, the bacteria enter them through certain precociously appearing stomata and pass into intercellular spaces, Soon there is differentiated in the leaf a special tissue composed of small cells rich in chlorophyll. Between these cells there develop capacious intercellular spaces, which the bacteria occupy henceforth. By the time the bacteria have occupied these spaces, the precocious stomata through which they entered the leaf become closed. From pure cultures of the host plants it was discovered that the bacterial tissue is derived from primordia which without the presence of the bacteria develop into a secretory reservoir, in which there accumulates a resin similar to that noted above as present in the bud. It is probable that the bacteria are attracted by this resin. Careful study of every stage in the life history of the host plants showed that the bacteria are always present. They become inclosed in the ovary at flowering,

[7] VON FABER, F. C., Über das ständige Vorkommen von Bakterien in den Blättern verschiedener Rubiaceen. Bull. Dép. Agric. Ind. Néerl. **46**: pp. 3. 1911. (See Bot. Centralbl. **119**:351. 1912.)

[8] ———, Das erbliche Zusammenleben von Bakterien und tropischen Pflanzen. Jahrb. Wiss. Bot. **51**:285–375. *figs.* 7. *pls.* 3. 1912.

and they enter the embryo sac through the micropyle. In seeds they occur constantly between the embryo and the endosperm. They are seen in young seedlings and in all later stages.

Careful study was made of the bacteria, both in the host plants and in artificial cultures. They were found to bear a close resemblance to the tubercle bacillus, both in structure and in behavior. Consequently VON FABER regards these organisms as members of the Mycobacteria, and he gives them the name *Mycobacterium Rubiacearum*, nov. sp. Of large interest also was the discovery that nitrogen is fixed in the artificial cultures of these organisms. VON FABER succeeded also in getting pure cultures of the Rubiaceae, the seeds being sterilized by placing them for 25 minutes in hot water at a temperature of 50°. The pure cultures grew far less vigorously than symbiotic cultures, and the leaves were lighter in color. It was observed also that nitrogen is fixed in the symbiotic cultures but not in the pure cultures, so that in nature these Rubiaceae can get their nitrogen supply directly from the air. Still further recalling the nutritive relations between the Leguminosae and their root bacteria is the fact that the bacterial tissue of the leaves of the Rubiaceae is rich in starch, which may serve the bacteria for food; there is evidence also of bacterial decadence, involution forms, and eventual phagocytosis. Pure cultures seem to indicate that each host species has its own bacterial "adaptation form."

MIEHE has also followed brief preliminary reports[9, 10] of his studies of hereditary symbiosis by detailed accounts.[11, 12] *Ardisia crispa*, one of the Javanese Myrsinaceae, has glandular thickenings on the leaf margins. These represent modified hydathodes and have commonly been regarded as albumen glands. It is now shown that these structures resemble ZIMMERMANN'S bacterial knots and are caused by bacteria. Furthermore the bacteria are present throughout the life history of *Ardisia*, and the details of bacterial entrance and subsequent behavior are astonishingly like those reported simultaneously in the Rubiaceae by VON FABER. The microorganisms enter the leaves through stomata, which later become closed. They were observed by MIEHE in the embryo sac, in the seed, and in the vegetation point of the seedling. Two species of bacteria have been isolated and are called *Bacillus foliicola* and *B. repens*. In old cultures there occur curved and branched involution forms. In most respects these organisms resemble VON FABER'S

[9] MIEHE, H., Die sogenannten Eiweissdrüsen an den Blättern von *Ardisia crispa* A.DC. Ber. Deutsch. Bot. Gesells. **29**:156–157. 1911.

[10] ———, Über Symbiose von Bakterien mit Pflanzen. Biol. Centralbl. **32**:46–50. 1912.

[11] ———, Die Bacterienknoten an den Blatträndern der *Ardisia crispa*. In Javanische Studien. Abhandl. Königl. Sächs. Gesells. Wiss. **32**:398–431. 1911.

[12] ———, Weitere Untersuchungen über die Bakteriensymbiose bei *Ardisia crispa* I. Die Mikroorganismen. Jahrb. Wiss. Bot. **53**:1–54. *pls. 2*. 1913.

Mycobacterium, except that there is no evidence of the fixation of nitrogen. Hitherto pure cultures of *Ardisia* have been unobtainable.

VON FABER[13] very recently has published further, checking up various minor points, and discussing MIEHE's work and his criticisms of the work of VON FABER. The most noteworthy result recorded in the latest paper is the success of the attempt to synthesize pure cultures of *Pavetta* and *Mycobacterium*. A symbiosis of the usual kind seen in nature resulted from the inoculation of the former by the latter. The luxuriant cultures thus arising seem to show clearly that VON FABER was working with the proper symbionts.—H. C. COWLES.

Stomatal activity.—ILJIN[14] has found that when the stomates of *Centaurea orientalis* are open, the guard cells have an osmotic pressure ranging from 85 to 108 atmospheres. When the stomates are closed, the guard cells have an osmotic pressure of 13–20 atmospheres. The osmotic pressure of the epidermal and parenchyma cells of the leaves vary little and approximate that of the guard cells with the stomates closed. Similar results were obtained for *Senecio Doria*, *Iris pumila*, *Eryngium campestre*, *Verbascum Lychnitis*, *Veronica incana*, and others. The guard cells with high osmotic pressure (stomates open) contain no starch, while the guard cells of low osmotic pressure (stomates closed) bear an abundance of starch. Conditions that bring about the closure of the stomates, darkness or excessive transpiration, will produce the condensation of the sugar to starch, accompanied by the great fall in osmotic pressure in about two hours. The reverse process of hydrolysis, accompanied by the great rise of osmotic pressure and opening of the stomates, is accomplished in about the same time under illumination and low evaporation power of the air. If these results are correct, we have here a great contribution to the mechanics of stomatal regulation. One would like to know the variation in the osmotic pressure of guard cells that show little stomatal regulation, as is true of certain swamp and xerophytic forms.

ILJIN[15] has also made an extensive study on stomatal regulation of transpiration. He used cuttings of plants in potometers and calculated the transpiration on the basis of the grams loss of water per 1000 cm.^{2} per hour. While the potometer measures water absorption rather than loss, he believes that the two quantities are essentially equal in his work, since he has always discarded experiments in which wilting became noticeable. He ran his experiments in the open, either in an exposed place (the steppe) or in a protected region

[13] VON FABER, F. C., Die Bakteriensymbiose der Rubiaceen (Erwiderung und ergänzende Mitteilungen). Jahrb. Wiss. Bot. **54**:243–264. *figs.* 3. 1914.

[14] ILJIN, W. S., Die Regulierung der Spaltoffnung im Zusammenhang mit der Veränderung des osmotischen Druckes. Beih. Bot. Centralbl. **32**:15–35. 1914.

[15] ———, Die Probleme des vergleichenden Studiums der Pflanzentranspiration. Beih. Bot. Centralbl. **32**:36–65. 1914.

(the ravine). On the steppe, *Sanguisorba officinalis* transpired more rapidly than *Clematis integrifolia*, 3.3 gm. against 1.2 gm. In the ravine the reverse was true, 1.7 gm. against 0.7 gm. Similar results were found for *Phlomis pungens* and *Ajuga Laxmanni*, with the former transpiring more rapidly in the steppe and less rapidly in the ravine. These facts are explained by the rapid closure of the stomates of *Sanguisorba* and *Ajuga* in the exposed position, and the slow closure in the other forms. In another experiment, two marked xerophytes, *Aster villosa* and *Veronica incana*, showed much higher transpiration than two evident mesophytes, *Aristolochia clematitis* and *Sanguisorba officinalis*. The losses in these forms were respectively 43.3, 15, 11.3, and 6.4 gm. These results are explained by the stomates being closed in the mesophytes and open in the xerophytes.

It was rather a common thing to find higher transpiration in a given mesophyte in the ravine than on the steppe, owing to the stomatal closure in the latter place. In *Ajuga Laxmanni*, there were 10.5 gm. on the steppe against 26.2 gm. in the ravine; in *Centaurea orientalis*, 17.6 gm. against 31.5 gm. In an experiment with *Helianthus annuus*, *Pisum sativum*, *Vicia Faba*, and *Polygonum fagopyrum* placed in a series of positions where the evaporation power of the air graded from a low value to a high, the transpiration rose with the evaporation power of the air up to a certain height, then it fell enormously with the rise of the evaporation power of the air. The break was the point at which stomatal closure was induced. When the author started with various mesophytes and xerophytes, all with the stomates open, and placed them in conditions where the evaporation power of the air was rather high and rising rapidly, as time elapsed the mesophytes showed rapid transpiration, rising rapidly with the evaporation power of the air for two hours or so, followed by a rapid fall. In this case there is a high and sharp pointed curve. The xerophytes showed slower initial transpiration, a far slighter rise with the evaporation power of the air, and no such marked fall. In this case, the curve is flat, with no very high or sharp point. ILJIN believes the two types of curves represent mesophytism on the one hand and adaptation for xerophytism on the other. The xerophyte can protect itself against excessive transpiration in exposed positions without curtailing extremely the CO_2 necessary for carbon assimilation by rapid or extreme stomatal closure. This work indicates the great importance of stomatal variation in regulating transpiration, especially in mesophytes, a conclusion quite in contrast with that of LLOYD.—WILLIAM CROCKER.

Alpine plant-geography.—RYDBERG,[16] in the first three of a series of articles on the phytogeography of the Rocky Mountain region, has discussed the alpine zone, its environmental conditions, geographic floristics, and plant

[16] RYDBERG, P. A., Phytogeographical notes on the Rocky Mountain region. I. Alpine region; II. Origin of the alpine flora; III. Formations in the alpine zone. Bull. Torr. Bot. Club **40**:677–686. 1913; **41**:89–103, 459–474. 1914.

communities. The first article characterizes the alpine zone as the area below perpetual snow and above the forest line, including for convenience the transitional area in which subalpine *Krummholz* and scattered trees alternate with alpine grassland. A number of the factors which together determine the position of timber line are discussed. The writer's opinion that deficiency of rainfall, or of precipitation in proper form, is an important factor preventing tree growth in the alpine zone may be questioned. In the table of precipitation for various points in Colorado given by ROBBINS (BOT. GAZ. **49**:260. 1910), Pike's Peak has the highest mean annual rainfall listed, 28.65 inches; July and August, when alpine plants are most active, are the rainiest months. The influence of mountain masses is given by RYDBERG as tending to moderate conditions, so as to allow trees to extend to higher elevations. This effect may not be so general, for some botanists believe the presence of surrounding mountain masses have the opposite influence in some cases. Few observers would agree with RYDBERG in classing Long's Peak, in the Front Range, with Pike's Peak and Sierra Blanca as isolated mountains. The question may be regarded as still open.

In the second article the regions in which the alpine species have probably originated (perhaps it would be better to say the geographic sources from which they have probably been derived) are discussed, with lists for each region and lists of species common to two or more regions. The author is of the generally prevalent opinion that most of our alpine plants reached their present scattered stations during glacial times, when the circumpolar arctic-alpine flora was practically continuous over much lower latitudes and altitudes than at present. More than one-third of the species are restricted to North America. About 100 species from the subalpine zone extend higher than the forest line, and the purely alpine plants number about 250 species.

The third article is an account of the associations. The communities are called formations (in the specific sense in which the term association is generally used); they are based on habitat as determined by topography. They are: (1) rock-slide formation of rock-slides and rock-fields; (2) the generally distributed mountain crest formation of areas thinly covered with gravelly soil (apparently this corresponds to the dry meadow of COOPER, BOT. GAZ. **45**: 324. 1908); (3) mountain seep formation; (4) alpine meadow; (5) alpine bog; (6) alpine lake or pond; (7) cliff formation; (8) snowdrift formation. It is perhaps a question whether some of the associations might not better have been characterized and named from the vegetation itself rather than from the habitat. The lists of species are full; those extending into the lower mountains are distinguished, and also those characteristic in, or confined to, the northern or southern parts of the Rocky Mountain region. Hardly any information is given to indicate which species are most frequent, abundant, or characteristic in particular associations. The alpine zone is really well known to very few botanists, and articles dealing with its vegetation are not numerous, thus giving the present writing so much the greater value.—ARTHUR G. VESTAL.

The mycorhiza of forest trees.—Some important experiments have been carried on by JOSEF FUCHS[17] with the mycorhiza of forest trees. The chief object of the experiments was the synthetic production of mycorhizas by bringing together pure cultures of the two symbionts. The trees employed were various conifers, and the fungi consisted of a number of humus-inhabiting forms. Most of the experiments gave negative results, but when six-month seedlings of *Pinus Strobus* were brought into contact with cultures of *Collybia macroura*, a strong development of endotrophic mycorhiza was secured. The finding in certain cultures of spores and mycelia quite unlike those used in the inoculations caused FUCHS to believe that root infection often may come from the seeds rather than from the substratum. *Picea* seedlings eight days old growing in sterilized humus had their roots infected by fungi. The infected cells of the conifer roots soon turned brown and were cast off, suggesting that the fungi are truly parasitic and not beneficial to the conifers. Frequently the invading fungi are deformed and killed by the protoplasm of the root. These results were obtained both with ectotrophic and with endotrophic mycorhizas.

W. B. MCDOUGALL[18] has made a careful study of the mycorhizas of a number of our common American trees, chiefly angiospermous species. Various forms of ectotrophic and endotrophic mycorhizas are described, both sorts being found on the same root in *Tilia americana*. In some cases the fungus species involved were identified, and it was observed that the mycelia of different species frequently can be distinguished from one another by differences in color and structure. Observations made at all seasons showed that mycorhizas are much more in evidence in autumn, winter, and spring than in summer, and hence are usually annual. The fungal symbiont in ectotrophic mycorhizas, so far as known, is almost always a basidiomycete, whereas this is rarely the case with endotrophic mycorhizas. Some mycorhiza fungi can inhabit several hosts and the host trees also may have several different mycorhiza fungi, but all mycorhizal fungi cannot form mycorhizas on all mycorhizal trees. Individual trees or parts of trees are often without root fungi, probably because the proper fungus species happens to be absent. The development of the mycelial mantle in the ectotrophic mycorhizas checks further root growth, whereupon branching takes place, resulting in the characteristic coralloid aspect of the small root branches. The author in discussing the theories of previous workers agrees with FUCHS (though not quoting him) that the fungi of ectrotrophic mycorhizas are ordinary parasites; these fungi are of no value to the trees, nor are they probably very harmful, since so many roots are without them, especially in the deeper soil layers. MCDOUGALL is less confident concerning the

[17] FUCHS, JOSEF, Über die Beziehungen von Agaricineen und anderen humusbewohnenden Pilzen zur Mycorhizenbildung der Waldbäume. Bibl. Bot. no. 76. pp. 32. *pls. 4.* 1911.

[18] MCDOUGALL, W. B., On the mycorhizas of forest trees. Amer. Jour. Bot. 1:51–74. *pls. 4. fig. 1.* 1914.

rôle of the fungi in endotrophic mycorhizas, as in *Acer*. The only adverse criticism to be made of this excellent paper concerns the mere detail of the use of the words symbiosis and heterotrophic. Heterotrophic is used for the case (*Tilia*) where the same root has ectotrophic and endotrophic mycorhizas, which certainly is not the usual sense of the word. Both McDOUGALL and FUCHS contrast parasitism and symbiosis, whereas etymology and the best usage make parasitism a kind of symbiosis.—H. C. COWLES.

Photo-growth reaction.—BLAAUW,[19] who has already proved himself a master in phototropism, now publishes an excellent piece of work on the effect of illumination on the growth of the sporangiophore of *Phycomyces*. He uses the term "photo-growth reaction" to indicate the changes in growth rate and amount caused by a single short application of light. He first works with equilateral illumination applied at right angles to the organ from four or eight directions. The quantity of illumination in the different experiments varies from 1 to 7,680,000 M.K.S. In all cases an early acceleration in growth is followed by a later retardation. In illumination of 16 M.K.S. and above the acceleration begins about 3.5 minutes after the beginning of illumination. In 1 M.K.S. it begins after 8 minutes, and in 6 M.K.S. after 6 minutes. The maximum acceleration was at about 7 minutes in 16 M.K.S. and above and later in lower quantities. Then follows a gradual fall in growth rate until a rate considerably below the normal is reached, and then a gradual rise until the normal rate is again reached. The duration, amount, and overlapping of these reactions vary much with the amount of illumination. In some of the lower light amounts the total acceleration exceeds the total retardation by threefold, while in the higher amounts the latter exceeds the former. This agrees with the finding of JACOBI that slight illumination (low intensities of medium duration or high intensities of short duration) accelerate growth, while medium or great amounts of illumination retard growth. JACOBI deals with only the difference of the accelerating and retarding effects, since she took her readings 24 hours after exposure. BLAAUW's work gives the continuous curves. In all the older works only the retarding effect had been reported. BLAAUW finds that for low light quantities, where the accelerating does not overlap the retarding effect, a quantitative relation can be found between quantity of stimulus and quantity of acceleration. The increased growth is proportional to the cube root of the light amount. JACOBI's conclusion that the quantity of stimulus law does not apply here is due to her failure to recognize that both effects (accelerating and retarding) appeared in every application, and that she was dealing only with their difference.

In a second group of experiments BLAAUW deals with phototropic response in the same organ, and with good evidence comes to the conclusion that phototropism in this form can be explained entirely by the total of the "photo-growth reactions." This brings us back to the old view of DE CANDOLLE under

[19] BLAAUW, A. H., Licht und Wachstum I. Zeitsch. Bot. 6:641–703. 1914.

a more complex garb. BLAAUW's work clearly indicates that the amount of effective light and not the direction of the ray is the determining factor in phototropism. He believes NOAK'S[20] opposing view is due to his overlooking the parabolic curve of the tip in the epicotyl of *Avena*, the shading effect of the sporangia of *Phycomyces* on the perceptive and growth regions of the sporangiophore, and the cylindrical lens effect of the latter organ. On account of its lens action the back of the organ in unilateral light is more strongly illuminated than the front. The matter is rendered more complex by the focal line lying at different depths with variation in the angle of the incident ray.—WILLIAM CROCKER.

The vegetation of Natal.—Perhaps no part of the world is theoretically more interesting and practically less known to the phytogeographer than South Africa, and it is a satisfaction to record the appearance of two excellent papers on the vegetation of Natal by Professor BEWS[21, 22] of the Natal University College. The first paper is of general nature, presenting the ecological factors and plant associations of the province as a whole. Although Natal is situated considerably to the south of the Tropic of Capricorn, much of the area is frostless and has a distinctly tropical vegetation. Especially is this true of the coast, where are to be found such tropical types as the mangroves and Pescaprae. Almost all of the coast line is fringed by dunes, reaching a height of 50–200 feet, and covered chiefly by xerophytic bush. The vegetation of the interior is mostly evergreen dicotylous forest and grassland. The forest (generally called bush) resembles SCHIMPER'S sclerophyll forests, except that they are in regions of summer rather than winter rain. Perhaps the most interesting type of bush is the yellow-wood bush, in which *Podocarpus* dominates. In the Natal bush epiphytes are relatively scarce, but lianas are very abundant. Transitional to the grassland or veld is the thorn veld, essentially a savanna, with a dominance of umbrella-shaped *Acacia* trees. In the veld the grasses are changing, largely because of human influences, and it is noteworthy that the invading grasses are less useful to man than the original grasses. A brief account is given of the marsh or vlei and of secondary associations, that is, those due to human influence.

The second paper is the initial one of a series contemplated by BEWS, dealing in detail with the vegetation of small areas in the province of Natal. In the veld the dominating natural grass is *Anthistiria imberbis;* increasing areas are being given over to the cultivation of wattle (*Acacia mollissima*)

[20] BOT. GAZ. **58**:88–89. 1914.

[21] BEWS, J. W., The vegetation of Natal. Annals of the Natal Museum **2**[3]:253–331. *pls. 10.* 1912.

[22] ———, An ecological survey of the midlands of Natal, with special reference to the Pietermaritzburg district. Annals of the Natal Museum **2**[4]:485–545. *pls. 7. map 1.* 1913.

and maize (known locally as mealie), and vast areas have been extensively modified by grazing and burning. In the modified veld *Aristida junciformis* largely replaces *Anthistiria*. The bush, vlei, and other types of associations are much less extensive about Pietermaritzburg than are those of the veld. The paper is accompanied by a map, indicating the areas occupied by the different associations.—H. C. COWLES.

The origin of coal.—A recent bulletin[23] from the Bureau of Mines presents the results of extensive researches as to the origin of coal, long a vexed question. WHITE discusses the geologic relations of coals, analyses of coal samples studied under the microscope, physiographic conditions attending the formation of coal, rate of deposition of coal, and regional metamorphism of coal. DAVIS contributes an account of the origin and formation of peat; while THIESSEN describes in detail the results of a microscopic study of coal, prefacing his account with a full historical review of the subject. The bulletin is so full of important facts and interesting inferences that it is impossible to recount them here, but some of the general conclusions may be mentioned.

An important conclusion is that all coal was laid down in beds analogous to the peat beds of today; and that all kinds of plants, in whole or in part, went into the deposit. The various materials entering into the structure of plants differ widely in their resistance to the various agencies that were concerned in peat formation and in the subsequent coal formation. At the death of the plants, dependent upon the conditions in the bog, a partial decomposition, maceration, elimination, and chemical reduction begins, brought about chiefly by organic agencies, mainly fungi at first, and later bacteria. Such labile substances as proteins are removed first, and the more resistant next, leaving the most resistant in the residue called peat. The various processes referred to above, conducted chiefly by biochemical agencies, are taken up and continued by "dynamochemical" agencies, through various later stages, resulting in the different grades of coal, as lignite, subbituminous, bituminous, cannel coal, and anthracite. "Coal, therefore, is chiefly composed of residue consisting of the most resistant components, of which resins, resin waxes, waxes, and higher fats, or the derivatives of the compounds composing these, are the most important." These substances perform mainly protective functions in plants, as in cuticles, spore exines (including pollen), bark, cork, and waxy coverings. A very interesting result of these investigations is that any algal origin of coal was not demonstrated, although this has been a conspicuous and perhaps favorite theory.—J. M. C.

Water requirement of plants.—The ratio of the amount of water taken up by a plant during its growth to the dry matter produced has been found to vary very much, and it would seem that its careful investigation would

[23] WHITE, DAVID, and THIESSEN, REINHARDT, The origin of coal. Bull. 38, Dept. Interior, Bureau of Mines. pp. x+390. *pls.* 54. 1913.

throw light upon the questions of what crop plants make most economical use of water and of what wild plants are best suited to their desert and semi-desert habitats. A former review[24] has called attention to the investigation of these problems by SHANTZ and BRIGGS during 1910 and 1911, while a more recent paper reports the results of the same investigators[25] obtained during the summers of 1912 and 1913. The investigations are remarkable for the extensive scale upon which they have been conducted, and for their duration throughout the growing season. More than 50 species have been the subjects of study, and for some the period of investigation extends over three years and includes many individual plants grown from seedling to maturity, the final result being the average of many determinations. As a rule, the same variety gave consistent results, although considerable differences were found between different varieties of the same plant; for example, the variety of alfalfa having the highest water requirement was nearly 50 per cent above the lowest.

Millet has proved throughout an excellent dry land crop, producing a unit of dry weight for every 310 units of water absorbed. It is closely followed by sorghum with a water requirement of 322, corn with 368, and sugar beet with 397; then come wheat with 513, barley with 534, oats with 597, alfalfa with 831, and others that it is impossible to enumerate here. Weeds show the greatest known range from such economic forms, as *Amaranthus* with 292, *Salsola pestifer* with 336, *Bouteloua gracilis* with 389, through such intermediate forms as *Xanthium commune* with 432, *Grindelia squarrosa* with 608, and *Helianthus petiolaris* with 683, up to *Ambrosia artemisiaefolia* with 948 and *Agropyron Smithii* with 1076. Like previous investigations by the same workers, this report contains a vast amount of exact quantitative data of value in studying the agricultural possibilities and the ecology of the great plains.—GEO. D. FULLER.

The origin and relationships of the Indonesian flora.—It is well known that WALLACE, basing his conclusions chiefly on animals, held to the idea of a sharp boundary line in the Straits of Macassar, separating the Indo-Malay and Australasian biogeographic regions. Not only were Borneo and Celebes thus separated biogeographically, but the line was supposed to separate such closely adjoining islands as Bali and Lombok, east of Java. Botanists generally have not found sharp lines between the Malay and Australian floras. HALLIER,[26] working under excellent auspices, finds that Asiatic types extend

[24] BOT. GAZ. **56**:514–515. 1913.

[25] BRIGGS, L. J., and SHANTZ, H. L., Relative water requirement of plants. Jour. Agric. Research **3**:1–63. *pls.* 7. 1914.

[26] HALLIER, HANS, Die Zusammensetzung und Herkunft der Pflanzendecke Indonesiens. Separate reprint from J. ELBERT'S Die Sunda-Expedition des Vereins für Geographie und Statistik zu Frankfurt am Main **2**:275–302. *figs.* 2. 1912.

far into Polynesia, fading out gradually instead of stopping abruptly. Similarly the Polynesian types extend into Indonesia, ceasing gradually and not suddenly. Thus phytogeographers are given more solid reasons than ever for opposing the view of WALLACE. Starting from this sure foundation, HALLIER sets out on the perilous task of constructing land bridges between present-day islands and continents. He believes that Indonesia, Australia, and Polynesia were once connected, the islands now existing having been the mountain peaks of this former continent. In still older times HALLIER believes that Australasia and Polynesia were connected by a wide land bridge with America, the northern boundary extending through the Sandwich Islands to Lower California and the southern boundary extending from the southern islands of New Zealand, south of the Society Islands, through Easter Island and Juan Fernandez to southern Chile. HALLIER'S views recall the submerged continent postulated by DARWIN in connection with his theory of the origin of coral islands; nowadays, however, geologists seem to be getting more and more convinced of the relative permanency of oceans and continents, at least throughout the more recent ages. The possibilities of plant migration in our present world are so very large that botanists may well leave to the zoologists the construction of extensive land bridges and the arbitrary submergence and emergence of continents.—H. C. COWLES.

Evaporation and plant succession.—Among the recent contributions of quantitative data concerning the factors causing the succession of plant associations is a study by WEAVER[27] of the evaporation conditions within certain grassland and forest associations of Washington and Idaho. The succession is from the prairie to a climax forest of cedar (*Thuja plicata*), and the record extends over 126 days beginning May 7, 1912. The average daily amounts of evaporation for the various associations taken in the order of their occurrence in the succession are, approximately, bunch grass 28 cc., prairie with southwest exposures 23 cc., prairie with northeast exposure 17 cc., yellow pine (*Pinus ponderosa*) 12 cc., fir-tamarack 9 cc., and cedar forest 8 cc. These atmospheric conditions are further compared, and using those of the mesophytic cedar forest as the standard of reference, it is found that "in the fir-tamarack association from May to September, atmospheric conditions in the lower stratum are 120 per cent as severe, in the average prairie of the plains 250 per cent, and in the bunch grass association 345 per cent as unfavorable for plant life as regards the evaporating power of the air." Moreover, the conditions in the mesophytic forest are found to be almost identical to those recorded by the reviewer[28] for the climax mesophytic forest of the eastern United States as determined in

[27] WEAVER, J. E., Evaporation and plant succession in southeastern Washington and adjacent Idaho. Plant World **17**:273–294. 1914.

[28] FULLER, G. D., Evaporation and plant succession. BOT. GAZ. **52**:193–208. 1911.

beech-maple forests of the Chicago region. Thus it is possible to make rather accurate comparisons of the conditions within the forests of the east and the west and to obtain quantitative demonstration of the equal mesophytism of the latter.

The differences in the evaporating power of the air in the different associations are found to be quite sufficient to show that this factor must be an important one in causing succession. Such accumulations of quantitative data as are contained in the present paper mark the advance of ecology along lines tending toward greater exactness, and it is to be hoped that they will become increasingly numerous.—GEO. D. FULLER.

Phylogeny of Filicales.—In continuing his studies of the Filicales, BOWER[29] has investigated *Blechnum* and its allies, and finds that the characters of the sori are of most importance in suggesting phylogenetic lines. The genus is treated in its wider sense, as comprising the subgenera *Lomaria*, *Salpichlaena*, and *Eu-Blechnum*. In *Lomaria* the indusium appears marginal, while in *Eu-Blechnum* it becomes apparently intramarginal owing to the formation of a new structure which BOWER calls the "flange." He produces evidence from a comparison of the development in numerous species that the protective organ is phyletically the same throughout the genus *Blechnum*, and he calls it the "phyletic margin." The general conclusions reached are as follows.

The *Blechnum*-like ferns and their derivatives represent a true phyletic sequence, which is traced to the region of the Cyatheaceae, the actual point of contact probably being *Matteuccia intermedia*, a fern of North China recently described by CHRISTENSEN. From this source several divergent lines have proceeded, the main line leading through § *Lomaria* to *Eu-Blechnum*, involving the origin of the "flange" and the diversion of the "phyletic margin" to indusial functions. Minor lines led to *Acrostichum*-like derivatives in *Stenochlaena* and *Brainea*. Interruption of the fusion sorus, occurring as an anomaly in *Blechnum*, led to the conditions shown in *Woodwardia* and *Doodia*. An outward arching of the fusion sorus of *Blechnum*, ultimately combined with interruption, gives the key to the origin of *Scolopendrium*. An outward swinging of the interrupted fusion sori, variously combined with archings and new formations of partial sori, and various branchings of the leaf, give the several types of *Asplenium*. The relation of *Plagiogyria* to the whole series is regarded as problematical, but it is suggested that it is an isolated and relatively primitive genus.—J. M. C.

Evolution of inflorescence.—PARKIN[30] has studied inflorescence from the evolutionary point of view, a subject which in his judgment has been "strangely

[29] BOWER, F. O., Studies in the phylogeny of the Filicales. IV. *Blechnum* and allied genera. Ann. Botany **28**: 363–431. *pls. 22–32. figs. 26.* 1914.

[30] PARKIN, J., The evolution of the inflorescence. Jour. Linn. Soc. Bot. **42**: 511–563. 1914.

neglected." Textbooks define inflorescences, but there has been no serious attempt to relate them from the standpoint of their evolution. Some of the conclusions from his comparative studies are as follows: flowers were originally borne on the plant singly, each terminal to a leafy shoot; from such a shoot, bearing foliage leaves below and ending in a single terminal flower, all inflorescences, as well as the solitary axillary flower, have probably arisen; two main classes of flower clusters are distinguished, which are named "apical" and "intercalary," the majority of inflorescences belonging to the former class, which includes the long recognized cymose and racemose types. The author carries these preliminary propositions forward into details as to how the various clusters have arisen. For example, the first flower cluster to arise from the solitary terminal flower is said to have been cymose in character. From this start various tendencies are traced, and among the results it follows that racemose inflorescences have proceeded from cymose ones, the panicle being the intermediate stage. In regard to the origin of solitary axillary flowers, the author proposes at least three different ways, all capable of being traced back to the solitary terminal flower. Throughout the presentation the genera showing the various stages in this evolution are cited.—J. M. C.

Ant plants.—ESCHERICH[31] adds further evidence against the now generally discredited theory of myrmecophily, through a study of *Humboldtia laurifolia*, one of SCHIMPER's typical myrmecophilous plants. Not only do the ants of *Humboldtia* offer it no protection, but they actually bring it harm by attracting woodpeckers. ESCHERICH notes that ants collect and store the bulbs of *Cyperus bulbosus*, and thus may be of significance in the dispersal of the species.

MIEHE[32] has carried on some interesting investigations on *Myrmecodia tuberosa*, one of the most famous of all "myrmecophilous" plants. It appears that the internal walls of the hollow tuber of this plant are in part smooth and yellow and in part warty and black. In the black warty areas the ants (*Iridomyrmex Myrmecodiae*) deposit their excrements, whereas they deposit their eggs in the smooth areas. The black patches owe their color to luxuriant growths of fungi, which doubtless get nourishment from the ant excrements. Possibly the ants use the fungi (which may be *Cladosporium* or *Cladotrichum*) as a source of food, since tufts of mycelia were frequently seen to be shaved off. The warty tracts develop independently of either ants or fungi and are pretty clearly shown to be organs of water absorption. MIEHE believes that the organization of these tubers was related originally to water absorption and accumulation, the ant relation being secondary and incidental.—H. C. COWLES.

[31] ESCHERICH, K., Zwei Beiträge zum Kapitel "Ameisen und Pflanzen." Biol. Centralbl. **31**:44–51. *figs. 2.* 1911.

[32] MIEHE, H., Untersuchungen über die javanische *Myrmecodia*. In Javanische Studien. Abhandl. Königl. Sächs. Gesells. Wiss. **32**:312–361. 1911.

———, Über die javanische *Myrmecodia* und die Beziehung zu ihren Ameisen. Biol. Centralbl. **31**:733–738. 1911.

Anatomy of the node.—An example of what sort of contribution may be made by real "comparative" anatomy to taxonomy is seen in SINNOTT's work on the node of Dicotyledons.[33] It has frequently been proposed to use the structure of the petiole in establishing relationships, but this region is subject to too great ecological variation to yield results of general significance. In the basal region of the leaf, however, a simpler and more constant condition is found, and the number of leaf traces is characteristic of great groups. With respect to the Angiosperms it is concluded that the primitive number of traces is three, and that evolution has taken place in two directions: (1) by increase, as in Umbelliflorae; and (2) by reduction to one trace, which appears to happen either by fusion of the original three or by disappearance of the two lateral strands, as may be seen in Cruciferae and Aquifoliaceae respectively. The correctness of these conclusions is attested by the occurrence of transitional forms and by the fact that seedlings frequently show a simpler condition of the leaf trace than does the adult. Such a study supports the validity of a number of ENGLER's orders, while it casts doubt on certain orthodox views, such as the near relationships of Compositae and Campanulaceae.—M. A. CHRYSLER.

Studies of desert vegetation.—SHREVE[34] has studied the influence of low temperatures on the distribution of the giant cactus, *Cereus giganteus*, and he concludes that the limiting factor in regard to distribution northward is the number of consecutive hours of freezing. Plants exposed experimentally to freezing for six to fifteen hours were not seriously injured, whereas an exposure of more than thirty hours to freezing temperatures resulted in death. It is concluded that the giant cactus cannot exist where an entire day occurs without thawing temperatures. Probably the distribution of many other plants of the warmer deserts are thus limited.

SHREVE[35] has studied also the establishment behavior of the palo verde, *Parkinsonia microphylla*. Out of 542 seedlings of the year 1910, observed in their natural habitats, only 62 remained alive at the end of sixteen months. Further observations showed that a number of seedlings die in the second and third years, whereas most plants attaining the age of three years are fairly established and live for a long time. Physical conditions, rather than competition with other plants, are the chief factor in producing these results, and the most important physical condition is the absorption-transpiration balance.—H. C. COWLES.

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[33] SINNOTT, E. W., Investigations on the phylogeny of the Angiosperms. I. The anatomy of the node as an aid in the classification of Angiosperms. Amer. Jour. Bot. **1**:303–322. *pls. 30–34.* 1914.

[34] SHREVE, FORREST, The influence of low temperatures on the distribution of the giant cactus. Plant World **14**:136–146. *figs. 3.* 1911.

[35] ———, Establishment behavior of the palo verde. Plant World **14**:289–296. 1911.

The plant life of Hartsville, South Carolina.—A delightful account of the flora of his old home town has been given us by COKER.[36] After a brief consideration of the climate, topography, and geology, the various plant formations are considered in turn as follows: sand hills, upland forests, flatwoods, savannas, bays and swamps, lakes and ponds. In the sand hills *Pinus palustris* still dominates; elsewhere its place has been taken largely by *Pinus Taeda*. The resistance of the former to fire is strikingly brought out. *Quercus Catesbaei* is one of the chief forms in the undergrowth. In the upland forests *Quercus falcata* and *Q. velutina* are dominant, although *Pinus palustris* once held an equal place with them. The flatwoods are poorly drained and also are dominated by pines and oaks. The savannas are essentially confined to undrained depressions in the flatwoods. The term bay, a folk-name of the coastal plain, is applied to shallow swamps and is contrasted with the deep swamps. More than half of the work is made up of an annotated list of the Hartsville plants, the trees being annotated more fully than the rest. The chatty, personal touch of this treatise recalls the charming volumes of the older naturalists, who followed in the train of GILBERT WHITE.—H. C. COWLES.

Evolutionary observations from New Zealand.—During the many years which COCKAYNE has devoted to ecological studies in New Zealand, he has, of course, observed many phenomena interesting from the point of view of evolution. These observations are now gathered together into compact form.[37] It is freely admitted that only through careful experiment can exact results be reached, though it is asserted that much valuable experimental material can best be disclosed by ecological study. COCKAYNE cites probable examples of elementary species, variation, and mutation. Epharmony is considered in detail, since it is felt that here is where ecology presents its most important contribution; convergent epharmony, as illustrated by divaricate shrubs, cushion plants, etc., in different families, is especially in evidence in New Zealand. Persistent juvenile forms have often been noted by COCKAYNE, and they are here set forth in some detail. In discussing the struggle for existence, it is noted that the 550 introduced species of New Zealand are by no means submerging the native flora, except in grazed or burned areas. The virgin timber is wholly free from these introduced elements.—H. C. COWLES.

Root characters, ground water, and plant distribution.—CANNON[38] has done much to orient our minds properly with relation to the characters and significance of roots. His discovery of the superficial root systems of cacti

[36] COKER, W. C., The plant life of Hartsville, S.C. pp. 129. *pls. 15*. Published by the Pee Dee Historical Association. Columbia, S.C. 1912.

[37] COCKAYNE, L., Observations concerning evolution, derived from ecological studies in New Zealand. Trans. N.Z. Institute **44**:1–50. *pls. 8. figs. 3*. 1912.

[38] CANNON, W. A., Some relations between root characters, ground water, and species distribution. Science N.S. **37**:420–423. 1913.

has altered our notions concerning the prevailing deep-rootedness of desert plants. In a recent short paper he brings further data along similar lines. The mesquite, as is well known, either may be a shrub or it may be a tree of considerable size. On flood plains, where it is a tree, its roots penetrate to the water table, whose depth may be 15–25 feet. Shrubby specimens on higher grounds have extensively spreading rather than deep roots. CANNON considers the root situation in different types of climate and makes several interesting suggestions.

In a brief note[39] CANNON calls attention to the somewhat curious fact that at Carmel, California, the removal of the chaparral undergrowth in forests of *Pinus radiata* is followed by the death of the pines. This is attributed to the shallow root system of the pines, which comes to grief when the soil is desiccated as a result of the removal of the chaparral.—H. C. COWLES.

Sand hill forestation.—Some government experiments of considerable interest to ecologists are being conducted in the sand hills of Kansas and Nebraska, as noted by BATES and PIERCE.[40] While the sand hills of Kansas are not extensive, almost a fourth of Nebraska is thus classified. Trees and even shrubs are not naturally very abundant in the sand hill region except along streams. In the planting a cue is taken from nature in the presence of *Pinus ponderosa* in the sand hill region; the occurrence of isolated tracts of this species suggests a former more extensive distribution. At the suggestion of Professor BESSEY, the Forest Service began planting as far back as 1891. About ten years ago, large tracts of land capable of forestation were set aside as national forests, and nurseries were established at Halsey, Nebraska, and Garden City, Kansas. In the Nebraska nursery, attention has been paid to conifers, and success has been had especially with *Pinus Banksiana* and the native *P. ponderosa*. In the Kansas nursery, experiment has been made chiefly with hardwoods.—H. C. COWLES.

The chemistry of symbiosis.—Not much is known concerning the exact chemical interrelations of symbionts. To ZELLNER it is a matter of surprise that investigators of symbiosis have paid so little attention to this fundamentally important feature, and he indicates in a brief paper[41] some of the places where more knowledge is urgently needed. Best known, of course, are the chemical interrelations existing between bacteria and Leguminosae. The significance of mycorhiza is much in dispute; ZELLNER'S view is that the fungi are water-absorbing organs for the roots. In the endotrophic forms phago-

[39] CANNON, W. A., A note on a chaparral-forest relation at Carmel, California. Plant World **16**:36–38. 1913.

[40] BATES, C. G., and PIERCE, R. G., Forestation of the sand hills of Nebraska and Kansas. Bull. 121, U.S. Forest Service. pp. 49. *pls. 13. fig. 1.* 1913.

[41] ZELLNER, JULIUS, Die Symbiose der Pflanzen als chemisches Problem. Beih. Bot. Centralbl. **28**[1]: 473–486. 1912.

cytosis is an important feature that should be looked into. As to lichens, it is noted that the chemistry of the plant complex is very different from the chemistry of the sum of the components, grown as separate individuals; the nutritive relations of the algal symbionts are not known. Similar suggestions are made relative to the need of investigating the chemistry of parasitism, as illustrated by ergot, wheat rust, and their host plants.—H. C. COWLES.

Lichens in relation to their substratum.—BACHMANN,[42] who for many years has paid attention to the substratum relations of lichens, has reported his observations on the lichens of granite and quartz. Granite is decomposed into a claylike substance by lichen tissue with some rapidity, the micaceous constituents being particularly subject to ready decay. The quartz elements, on the other hand, are extremely resistant to such decomposition.

In a later paper BACHMANN[43] reports the results of studies on calcareous lichens with *Chroolepus* gonidia. He finds that the *Chroolepus* itself is able to dissolve calcium carbonate, so that after a time a limestone becomes perforated in spongelike fashion through the agency of the *Chroolepus* cells of the fungal hyphae. As soon as the *Chroolepus* cells become inclosed by hyphae, they bud in a yeastlike manner and take on bizarre forms. On account of its position within a rock, such a lichen retains moisture longer than do ordinary superficial lichens.—H. C. COWLES.

Taxonomic notes.—WERNHAM[44] has described a new genus (*Neosabicea*) of Rubiaceae from Colombia. It belongs to the tribe Mussaendeae.

DÜMMER[45] has described two new species of *Callitris*, one from New Caledonia and the other from the mountains of Ngoye.

BENEDICT[46] has begun a revision of the genus *Vittaria*. The first paper is a discussion of seven species, representing the subgenus *Radiovittaria*, and includes two new species.

BAKER[47] has published a study of the African species of *Crotalaria*, preceding the descriptive list by a historical introduction, and also a discussion of the delimitation of the genus. The paper recognizes 309 species, the genus extending from Egypt and the Soudan and the Sahara to Cape Colony in the

[42] BACHMANN, E., Die Beziehungen der Kieselflechten zu ihrer Unterlage. II. Granat und Quarz. Ber. Deutsch. Bot. Gesells. **29**:261–273. *figs. 4.* 1911.

[43] ———, Der Thallus der Kalkflechten. II. Flechten mit Chroolepugonidien. Ber. Deutsch. Bot. Gesells. **31**:3–12. *pl. 1.* 1913.

[44] WERNHAM, H. F., New Rubiaceae from tropical America. Jour. Botany **52**: 225–277. *pl. 533.* 1914.

[45] DÜMMER, R. A., Three Conifers. Jour. Botany **52**:236–241. 1914.

[46] BENEDICT, R. C., A revision of the genus *Vittaria* J. E. Smith. Bull. Torr. Bot. Club **41**:391–410. *figs. 7. pls. 15–20.* 1914.

[47] BAKER, E. G., The African species of *Crotalaria*. Linn. Soc. London. Bot. **42**:241–425. *pls. 9–14.* 1914.

south. In the list there are included descriptions of 76 new species and varieties.—J. M. C.

Flora of Shikotan.—TAKEDA[48] has studied somewhat intensively the flora of Shikotan, which is a small island situated near enough to the Kurile Islands to be regarded as one of them, at least in climatic conditions. The great interest of the islands in general is that the vegetation is quite primeval, nothing having been disturbed by the hand of man; in fact, Shikotan seems not to have been touched by human hands at all. An analysis of the floristic features is presented, and the enumeration includes 234 species, the largest assemblage being dicotyledons (219). The four largest families appear in the following order of abundance: Compositae, Gramineae, Rosaceae, and Umbelliferae. The largest genus is *Carex*, with 15 species; and 28 families are represented by a single genus, 23 of these genera being represented by a single species. The list includes the description of 5 new species.—J. M. C.

Phytogeographic notes from Palestine.—AARONSOHN[49] has called attention to some species that are disappearing from the flora of Palestine. He describes a little known station of *Acacia albida*, a species of northern Africa heretofore regarded as merely cultivated in Palestine. AARONSOHN regards it as an indigenous relict. Among other rare relicts in Palestine are *Pinus halepensis*, *Juniperus phoenicea*, and *Fraxinus oxycarpa oligophylla*. The author believes that these species, on account of the great need for wood in the arid Palestine climate, have been essentially exterminated by man. An interesting argument in support of this view, recalling the methods employed by the English ecologists in working out the original distribution of the beech, is based on the occurrence of place-names derived from these trees in neighborhoods where these species are no longer to be found.—H. C. COWLES.

U.S. Forest Service.—Among various articles of more or less general interest in a recent periodical, JAENICKE[50] gives a brief and interesting résumé of the varied activities of the Forest Service. This organization, employing the services of 2,895 persons, many of them with botanical training, and expending annually some $6,000,000, devotes its attention to subjects ranging from purely botanical research through reforestation and forest protection to the sale of timber and the development of water power. With increasing interest in forest protection, there is coming an increasing demand for increasing

[48] TAKEDA, H., The flora of the island of Shikotan. Jour. Linn. Soc. Bot. **42**: 433–510. 1914.

[49] AARONSOHN, A., Notules de phytogéographie palestinienne. (I). Une station peu connue de l'*Acacia albida* Del. (II). Espèces en voie d'extinction. Bull. Soc. Bot. France **60**:495–503, 585–592. *pl. 1*. 1913.

[50] JAENICKE, A. J., Progress of the U.S. Forest Service as reflected in the forester's reports of 1911, 1912, 1913. Forestry Quarterly **12**:397–407. 1914.

efficiency and more scientific knowledge of the principles underlying the various phases of forest administration, and these demands are being met as far as the limited funds permit.—GEO. D. FULLER.

Parasitic fungi of Wisconsin.—DAVIS[51] has brought together in a single list the parasitic fungi of Wisconsin reported in a succession of previous lists, beginning with that of A. F. BUNDY, published in the Report of the Geological Survey issued in 1873–1879, and including 30 species. The next list was that of TRELEASE (1884), and since then DAVIS has been indefatigable in adding species which justified the publication at intervals of supplementary lists. The final list contains 825 species of parasitic fungi and about 750 hosts. The Phycomycetes are represented by 61 species, 24 of which belong to *Peronospora*. The Ascomycetes number 502 species, the largest genus being *Septoria*, with 121 species. The Basidiomycetes number 256 species, all but 6 of which are smuts and rusts.—J. M. C.

Sand dune plants.—In a study of the flora of some sand dunes near the sea between Redonda and Venice, California, COUCH,[52] has made a floristic census of a number of quadrats, showing that in this area *Gaertneria bipinnatifida* is the dominant pioneer plant, but as the succession advances with increasing stability of the substratum, it is succeeded by *Abronia umbellata*, which is closely followed by *Eriogonum parvifolium*, *Adenostoma fasciculatum*, *Cheiranthus suffrutescens*, and *Lupinus Chamissonis*. Attention is also directed to the two kinds of competition here evident, that between the plants and their environment, and that between the plants themselves.—GEO. D. FULLER.

Antagonistic symbiosis in lichens.—TREBOUX'[53] studies of *Cystococcus humicola*, an alga that occurs free in nature and also in symbiosis with lichen fungi, lead him to the view that the lichen fungus is essentially parasitic. He concludes that the physiology of this alga is the same, whether inside or outside of a fungal symbiont; it does not require protein food (peptone) in either case, but can secure its nitrogen from nitrates or ammonium salts. Among the points in favor of the theory of parasitism are the smaller size of the symbiotic algae as compared with the free algae, less frequent cell division, diseased aspect where in contact with haustoria, and the relative absence of pyrenoid starch.—H. C. COWLES.

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[51] DAVIS, J. J., A provisional list of the parasitic fungi of Wisconsin. Trans. Wis. Acad. Sci. **17**:846–984. 1914.

[52] COUCH, E. B., Notes on the ecology of sand dune plants. Plant World **17**:204–209. 1914.

[53] TREBOUX, O., Die freilebende Alge und die Gonidie *Cystococcus humicola* in Bezug auf die Flechtensymbiose. Ber. Deutsch. Bot. Gesells. **30**:69–80. 1912.

The vegetation of California.—CANNON[54] has published the address on the vegetation of California in relation to environment, which he delivered in 1913, at Carmel, California, before the members of the International Phytogeographic Excursion. The California environment is highly specialized, owing to the great climatic diversity, which in turn is associated with physiographic complexity. The corresponding specialization of the vegetation is shown in the marked vegetational types and also in the large display of endemism. An example of another sort of specialization is brought out in a consideration of the root relations of the oaks.—H. C. COWLES.

Branching of Rhizophora roots.—The repeated branching of the prop roots of *Rhizophora* is well known and has often been described. DOCTERS VAN LEEUWEN[55] has made the remarkable discovery that this branching is not a fixed feature of the roots, but is caused by an unidentified Scolytid beetle, which eats the growing portion of the roots. The destruction of a growing root tip is followed by the appearance of a lateral branch, about a centimeter above the killed portion. One plant was found far from the sea, in which an uninjured root grew down to the ground without branching.—H. C. COWLES.

Bees and cotton blossoms.—Stimulated by the discordant views as to the office of flower color in the attraction of insects to flowers, H. A. ALLARD[56] has made a series of observations on the visitation of cotton blossoms by bees, especially by *Melissodes*. It is concluded that the showiness of the flowers is the chief factor determining the insect visits. The removal or covering of the petals greatly reduces the number of visits. Only 12 per cent of the flowers inspected by bees were actually entered by them. Evidence is given of the influence of associative memory.—H. C. COWLES.

Polyporaceae of Ohio.—OVERHOLTS[57] has published a monograph on the Polyporaceae of Ohio, with full descriptions and keys. Approximately 100 species are described, representing 10 genera. One of the features of the monograph is that the descriptions are exactly comparable with one another, so that the contrasting characters are brought out with unusual clearness.—J. M. C.

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[54] CANNON, W. A., Specialization in vegetation and in environment in California. Plant World **17**:223–237. *figs.* 3. 1914.

[55] DOCTERS VAN LEEUWEN, W., Über die Ursache der wiederholten Verzweigung der Stützwurzeln von *Rhizophora*. Ber. Deutsch. Bot. Gesells. **29**:476–478. *figs.* 2. 1911.

[56] ALLARD, H. A., Some experimental observations concerning the behavior of various bees in their visits to cotton blossoms. Amer. Naturalist **45**:607–622, 668–685. 1911.

[57] OVERHOLTS, L. O., The Polyporaceae of Ohio. Ann. Mo. Bot. Garden **1**:81–155. 1914.